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Inheritance of quantitative traits in inter and intraspecific crosses of barley

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by

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INTRODUCTION

Modes of inheritance of agronomic traits have been intensively studied in cultivated Hordeum L., but few such studies have been reported for interspecific crosses in this genus. First attempts to obtain hybrids between wild and cultivated barley species were made in the 1880's by Bestehorn (as cited in Bakhteyev and Darevskaya, 1960). Subsequently, several investigators made interspecific hybrids in Hordeum for theoretical studies.

Introgression of germplasm from wild into cultivated barley populations should be of interest to barley breeders because it is a method to broaden and diversify the breeders's gene pool. Recently, Lawrence (1974) showed that introgression of genes from Avena sterilis into A. sativa (cultivated oats) via backcrossing made it possible to improve grain yield by 20-30 percent. Based on this experience with oats, similar research has been initiated with barley at the Iowa Agriculture and Home Economics Experiment Station. As a part of this program, I used H. vulgare and H. spontaneum for interspecific crosses to explore such hybrids as an alternative to intraspecific crosses for improving this crop.

Whether source populations of self-pollinated species in which plant breeders practice selection originate from intra or interspecific crosses, the source or reference populations need to be analyzed to describe gene action and other genetic parameters to provide the information necessary for a plant

breeder to choose the best parents, the best selection procedures, and to decide what variety type will be developed.

The specific objectives of my investigation were to:

(1) evaluate the relative magnitudes of additive, dominance and epistatic genetic effects and the heterosis for several quantitatively inherited traits in intra and interspecific crosses of barley;

(2) estimate the minimum number of effective factor pairs that control the expression of these quantitative traits in intra and interspecific crosses;

(3) explore the relative proportions of transgressive segregates in intra and interspecific crosses;

(4) use information about inheritance in intra and interspecific crosses to predict the most desirable level of germplasm introgression from H. spontaneum into breeding populations of cultivated barley; and

(5) study the associations among several quantitative traits in barley.

LITERATURE REVIEW

Inheritance Studies in Barley

Barley has been the subject of intensive genetic studies due to its many contrasting traits, its diploid status and low chromosome number (n = 7), its autogamous reproduction, its annual habit, and the ease with which cultivated and some wild forms can be hybridized (Cook, 1962). The literature on inheritance of barley is very extensive, but I will review only those papers that have a direct bearing on the traits involved in my study.

Robertson et al. (1941,1947), Smith (1951), and Nilan (1964) compiled detailed bibliographies on modes of inheritance and linkage relationships in barley, but insofar as I can determine, study of the inheritance of yield has not been reported recently.

Griffee (1925) found that maturity was controlled by a single factor pair and earliness was dominant. Maturity was strongly linked to a locus that controlled reaction to Helminthosporium sativum. Harlan and Martini (1929) concluded that late varieties may contain factors for earliness, and Wexelsen (1933) found that two factor pairs determined date of heading. According to a review by Smith (1951), earliness in barley has been reported both as a dominant and as a recessive trait, and to be governed by genes at one, two, three, or more loci depending upon the varieties crossed. Two criteria, date

of heading and date ripe, have been used by barley breeders to determine maturity, but because the interval between these two phenomena is constant, either is satisfactory for measuring maturity (Frey, 1954).

Ubisch (1919) reported that culm height was governed by genes at one to three loci in barley. Neatby (1926) studied plant height in a F_2 population of barley and concluded that two or more factor pairs conditioned plant height. Later, he (Neatby, 1929) reported that plant height was controlled by factors at four or more loci and that inheritance of days to maturity was controlled by three factor pairs. Lorenzetti and Ceccarelli (1975) found that tallness was dominant.

David (1931) crossed Trebi with three smooth-awned varieties of barley, and found the heights of the F_1 hybrids approached those of the taller parents. Parental forms were recovered easily in the F_2 and F_3. In two crosses, days to flowering and plant yield were negatively correlated, whereas number of culms and plant height were significantly and positively associated with yield.

Grafius (1938) crossed Velvet and Spartan varieties, and in the F_2, he found a positive correlation between plant height and grain yield, and further, 2-rowed types were taller than their 6-row counterparts. Kohl (1930) and Robertson and Koonce (1936), working with varieties, found positive correlations between yield and plant height. Leasure et al. (1948) reported that correlations of plant height, head length, straw break-

ing strength, and test weight with yield were significant but small.

In Iowa, Hehn (1948) found that in spring x spring barley crosses, earliness was governed by one to three major factor pairs, whereas in winter x spring crosses, a large number of F_2 segregates were earlier than the spring varieties. These resulted from a cumulative type of gene action between the dominant growth-factor allele, Sh_2, and the dominant earliness allele, Ea_3.

Recently, Fasuolas and Allard (1962) found that additive genetic variance accounted for 43, 89, 72 and 72 percent of the genotypic variance of heading time, plant height, number of spikes, and yield of spikes, respectively, in barley. Epistatic variance accounted for 52 and 100 percent of the genotypic variance for heading date and yield of spikes. Dominance variance was very small for all traits. Grafius et al. (1952) found that additive genetic variance for yield was small whereas the non-additive fraction was large in bulked F_2 progenies of barley. Also, Johnson and Aksel (1958) found a large amount of dominance relative to additive variance for yield in barley.

Abo-Elenein et al. (1975) showed that kernel weight was quantitatively inherited. Transgressive segregation occurred for both heavy and light kernel weights, and there were epistatic effects in all crosses. In contrast, Riggs and Hayter (1975) detected high and positive dominance in the F_1 for

1000-kernel weight.

Barbacki et al. (1976) indicated that transgressive segregates may be of evolutionary and practical value in barley.

Heterosis in Barley

The first study of hybrid performance in barley was done by Engledown and Pal (1934) who observed only a few crosses with apparent hybrid vigor. Immer (1941) found that the mean of F_1's from six crosses exceeded the parent average by 4.9 percent for weight per seed and 27.3 percent for plant yield. Heterosis for seed size was reported by Immer (1942). Suneson and Riddle (1944) found average yield heterosis of more than 20 percent in three of seven F_1's; however, Hagberg (1953) could show no heterobeltiosis for grain yield in 17 hybrids, but whole plant weight of the F_1's often was equal or superior to the better parent, especially for crosses between two and six-rowed varieties. The 1000-seed weight of F_1's was about 20 percent higher than the weight of the two-rowed parents, i.e., varieties with the heavier seeds. Sakai and Gotoh (1955), comparing 10 F_1's with their parents, found heterosis for plant weight and spike weight. The 15 F_1 hybrids between six-rowed spring barley varieties studied by Grafius (1959) exceeded the parent mean by 3.7 percent in kernel weight and 35.9 percent in grain yield. Because correlations between spikes per plant, seeds per spike, and kernel weights

were either small or zero, he argued that there were no genes for yield per se but only genes for the yield components. He concluded that the F_1 vigor for yield in barley was due to epistasis.

Aastveit (1961) found heterobeltiosis for total and grain yield and weight of 1000 grains in one barley cross. According to Suneson (1962), the average degree of heterobeltiosis in F_1's of barley was 20-30 percent and the increased yields in all crosses were due to increased tillering. Pawlisch and Van Dijk (1965) found some barley hybrids had higher yielding capacities than the best available pure lines.

Using 28 hybrids in F_1 and F_2, Upadhyaya and Rasmusson (1967) found significant heterosis for grain yield, kernel weight, kernels per spike, spikes per plant, and plant height. The average heterobeltiosis for grain yield was 9.1 percent, but the mean depression from F_1 to F_2 was 26.1 percent.

Carleton and Foote (1968) found no heterosis for yield in twelve hybrids, and hybrid performance in a study by Peterson and Foster, 1968, as cited in Stolen (1974) showed heterobeltiosis ranged from 3 percent in the Trophy x Trebi cross to 25 percent in the Trebi x Barbless cross.

The literature indicates the existence of heterosis and even heterobeltiosis in barley. And, hybrid barley has been an objective of barley breeders for many years, but obtaining high and consistent cross-pollination to produce large quanti-

ties of hybrid seed constitutes a major problem not yet solved for hybrid barley.

Introgression of Germplasm from Weedy Relatives into Cultivated Barley

The term "introgressive hybridization" was used by Anderson and Hubricht (1938) to denote the gradual transference of genes from one species into the germplasm pool of another as a consequence of natural or artificial hybridization and repeated backcrossing. Anderson (1949) and Stebbins (1959) believe that introgression of germplasm from weedy relatives has been an important feature in the natural evolution of many cultivated species. For example, there is good evidence that maize (Zea mays L.) has absorbed some characteristics from teosinte (Zea mexicana Schrad.) and Tripsacum, through a system of natural introgression (Mangelsdorf, 1952; Mangelsdorf, McNeish and Galinat, 1964; De Wet and Harlan, 1972). Zohary (1963) pointed out that wild, brittle, two-rowed H. spontaneum occasionally hybridizes with cultivated, six-rowed H. vulgare and well-developed "swarms" usually contain parental forms and a whole array of intermediates and recombinants. The main objective of artificial interspecific hybridization involving cultivated species is to duplicate in a short time what may be accomplished in natural evolution in a much longer time span.

Generally, when wild or weedy relatives have been used as

germplasm sources to improve cultivated crops, it was for the purpose of obtaining pest resistance genes. Rajhathy et al. (1963) said that interspecific research is necessary in a breeding program only when the variation within the cultivated species is exhausted or if important genes are not available in the cultivated germplasm.

Only a few plant breeders have explored the possibility of using weedy relatives as a source of genes for increasing yield of cultivated crops (Frey, 1976; Reeves, 1950; Reeves and Bockholt, 1964; Efron and Everett, 1969; and Harlan, 1976). That weedy species can be a valuable source of favorable genes for improving agronomic traits has been reported by Lawrence and Frey (1976) for oats (A. sativa L.). In Iowa, introgression of germplasm from A. sterilis, a weedy relative that abounds around the Mediterranean sea, has contributed genes that increase yield in cultivated oats by 25 to 30 percent.

To detect potentially useful genes in weedy species for improving cultivated crops, certain studies on genetic relationship are needed. Harlan and De Wet (1971) have proposed a system of classification of cultivated plants and their relatives based on the crossability among them. According to their classification, H. vulgare and H. spontaneum belong to the same primary gene pool. Likewise, Rajhathy et al. (1963) considered H. spontaneum as a form (or specie) included in H. vulgare because they do not have reproductive isolation. On the other hand, Bakhteyev (1963) considered that H. spon-

taneum was an ancestor of cultivated barleys. Vavilov (1926) was reluctant to assign H. spontaneum the role of progenitor for all cultivated barley because he felt that it was not sufficiently variable to account for the great range of diversity in the crop. Harlan (1970) mentioned, however, that the subspecies spontaneum is decidedly more variable than Vavilov appreciated. He concluded that barley was domesticated from vulgare ssp spontaneum in the Near East during the eighth millennium B.C.

MATERIALS AND METHODS

Genetic Materials

Twelve crosses (six intraspecific and six interspecific) involving six Hordeum vulgare L. cultivars and three H. spontaneum collections were used in this study (Table 1-2). Three monogenic recessive male-sterile stocks of spring barley, H. vulgare L. were used as females (Hockett et al. 1968) to facilitate crossing.

Because all generations needed to be compared in a uniform cytoplasmic background, all single-cross F_1's were made using the H. vulgare varieties as females and first backcrosses to H. spontaneum were obtained using F_1's as females. For each cross the following seven generations were obtained: F_1, F_2 and F_3 from the single crosses, B and B′ which were backcrosses of F_1's to P and P′, respectively, and BS and BS′ were the selfed progenies from the backcross B and B′, respectively. All single and backcrosses were made in the greenhouse during the winter seasons of 1976-77 and 1977-78.

In 1977, about 100 F_2 seeds from each of six crosses (i.e., intraspecific crosses 2, 4, and 5 and interspecific crosses 7, 8, and 12) plus 15 seeds from each parent were space planted in the field to produce F_2-derived and parental lines.

The various generations and lines from the 12 barley crosses were used in experiments in the controlled-environment chamber and in the field.

Table 1. Varieties and lines of barley used as parents

Accession No	Strain	Species	Description or classification	Source
B639	Betzes	Hordeum vulgare	Male sterile stock 89	Eslick
B630	Unitan	Hordeum vulgare	Male sterile stock 63	Eslick
B631	Trophy	Hordeum vulgare	Male sterile stock 42	Shands
B632	M-25	Hordeum vulgare	Experimental line	Rasmusson
B633	M-31	Hordeum vulgare	A semi-dwarf experimental line	Rasmusson
B634	Manker	Hordeum vulgare	Variety	Rasmusson
B661	PI 227301	Hordeum spontaneum	Gentry HS	Iran
B662	PI 227019	Hordeum spontaneum	Gentry HS	Iran
B663	PI 296870	Hordeum spontaneum	Dinoor A680	Israel

Table 2. Parents and accession number for the twelve barley crosses used in this study

Cross number	Female parent		Male parent
1[a]	Betzes	x	M-25
2[a]	Betzes	x	M-31
3[a]	Betzes	x	Manker
4[a]	Unitan	x	M-31
5[a]	Unitan	x	Manker
6[a]	Trophy	x	M-25
7[b]	Betzes	x	PI 227301
8[b]	Betzes	x	PI 227019
9[b]	Betzes	x	PI 296870
10[b]	Unitan	x	PI 227301
11[b]	Trophy	x	PI 227019
12[b]	Trophy	x	PI 296870

[a]Intraspecific crosses.
[b]Interspecific crosses.

Controlled Environment Experiment

One experiment involving all 12 parental combinations was conducted in a controlled-environment chamber during August-November 1977 to estimate the magnitudes of various genetic effects on the expression of six traits via a generation-means analysis. The experimental design was a randomized complete-block with three replicates. A plot was a pot with one plant. Each replicate contained: (a) two plants of each of the nine parents and 12 F_1's, (b) three plants of each of the 24 backcross F_1's, and (c) four plants of each of the 12 F_2's.

The growing medium was a 1:1:1 mixture of peat, sand, and loam. Granulated fertilizer (1/4 tsp. of 6:10:4 analysis) was applied to each pot before and thirty days after planting. Water was applied daily and plants were tied to bamboo stakes to prevent lodging. The chamber was lighted with fluorescent and incandescent lamps for 16 and 15 hours day, respectively. Day and night temperatures were 21° and 18.5°C, respectively.

Traits measured on an individual plant basis were: (a) heading date recorded when the first spike of a plant was completely emerged, (b) plant height as cm from the growing-medium surface to the spike tip, (c) number of spikes per plant, (d) straw yield, (e) grain yield, and (f) harvest index, i.e., grain yield divided by total plant yield.

Field Experiments

In summer 1978, I conducted twelve experiments in the field at the Agronomy Field Research Center near Ames, Iowa for the generation means analyses. Each experiment contained six generations, i.e., P, P′, F_2, F_3, BS and BS′ from one parental combination (Table 2). Each experiment was grown in a randomized complete-block with five replicates.

Another experiment with 360 F_2-derived lines in F_3 representing 60 lines per cross for six crosses, i.e., intraspecific crosses 2, 4, and 5 and interspecific crosses 7, 8, and 12, plus 15 lines for each of the eight parents were tested in the field in a randomized complete-block design with three replicates. In all 13 experiments, a plot contained 15 seeds sown in a hill, and the hills were spaced 30 cm apart in perpendicular directions (Frey, 1965; Ross and Miller, 1955).

In each field experiment six traits were measured on a plot basis. Heading date was recorded when half the spikes in a plot were fully emerged. Plant height (cm) was measured as the distance from the ground surface to the tips of majority of the spikes. At maturity, the plants in a plot were cut, dried and weighed to give bundle weight (g). Next, the bundle was threshed and the grain yield was recorded (g). Harvest index was calculated as the ratio of grain yield to bundle weight. Also, 300-seed weight was measured on a sample from each plot.

Occasionally, a plot representing a backcross, F_2, or F_3 generation contained a few male sterile plants, in which case the plot was considered missing for the analyses of grain yield and harvest index, in a few instances, the proportion of male sterile plants in the hill was more than 20 percent.

All plots were sprayed with a fungicide[1] at weekly intervals from anthesis to maturity to control foliar fungal diseases that could have affected grain yield. Prior to maturity all plots of H. spontaneum parents and all generations derived from crosses involving this species were covered with mesh bags to prevent seed loss due to shattering.

Analytical Procedures

Generation mean analysis

The first step in the examination of data from the controlled environment experiment and the first 12 field experiments was to perform an analysis of variance of all generations for each cross to determine whether significant differences existed among the generation-means. If significant difference did not exist among generations in a parental combination, it indicated that no differences among generations was not different from zero for the trait. If the analysis of variance indicated significant differences among generation means, I next analyzed the generation means by using the procedure outlined by Hayman (1958).

[1]Dithane M-45

I used Gamble's (1962) notation in defining parameters because the meaning of this notation is more readily apparent than that used by Hayman (1955, 1958, 1960):

Genetic effect	Hayman"s notation	Gamble's notation
Additive (Add)	[d]	[a]
Dominance (Dom)	[h]	[d]
Add x Add epistasis	[i]	[aa]
Add x Dom epistasis	[j]	[ad]
Dom x Dom epistasis	[l]	[dd]

The generation-means analysis was begun by fitting the additive model (i.e., $m + \alpha_i[a]$) to the data for a trait from the various generations from a parental combination. Next, the deviations from the additive model were tested for significance via error term or Chi-square for goodness of fit. If the deviations were significant, the next model fitted to the data was additive plus dominance (i.e., $m + \alpha_i[a] + \beta_i[d]$) and again, the deviations from the model were tested for significance. This procedure was continued with successive additions of [aa], [ad], and [dd] terms until either (a) no significant deviations occurred or (b) all genetic effect terms had been used in the model.

The generation-means model shows only the summation of ef-

fects for all genes affecting a trait, and it does not permit the measurements of individual gene effects. Because variances of the means of different generations were unequal, all generation means and their expectations had to be weighted. The procedure outlined by Hayman consists of estimating the parameters by weighted least squares using as weights the reciprocals of the variances of the means. The comparison between expected and observed means can then be effectively approximated by assuming the sum of squares minimized in the fitting process is distributed as χ^2 with degrees of freedom equal to the number of means minus the number of parameters involved in the model. Therefore, the goodness-of-fit for the sequential model can be tested by squaring the deviation of the observed from the expected value for each generation, multiplying by the corresponding weight, and summing the product over all six generation types. The degrees of freedom for the χ^2 is the number of generations minus the number of genetic effects involved in the model.

The first model to be fitted was:

$$Y_i = m + \alpha_i [a] + E_i$$

If the deviation from this model, which included only the additive effects, was significant, the following general non-epistatic model was used:

$$Y_i = m + \alpha_i\,[a] + \beta_i\,[d] + E_i$$

This model includes the mean of F_2, additive effects, and dominance effects. In the absence of epistasis, the estimates of additive and dominance effects are meaningful and unbiased by linkage disequilibrium. When epistasis was present the digenic model for a generation mean was:

$$Y_i = m + \alpha_i\,[a] + \beta_i\,[d] + \alpha_i^2\,[aa] + 2\,\alpha_i\,\beta_i\,[ad] + \beta_i^2\,[dd]$$

where:

m = mean of the F_2 or reference generation,

[a] = pooled additive effects of the genes,

[d] = pooled dominance effects of the genes,

[aa] = pooled additive by additive effects of the genes (homozygote x homozygote digenic interaction),

[ad] = pooled interaction between additive and dominance effects of the genes (homozygote x heterozygote interaction),

[dd] = pooled interaction between dominance effects of the genes (heterozygotes x heterozygotes digenic interaction),

α_i and β_i were the appropriate coefficients for the additive and dominance effects for these generations. The coefficients of the components of the generation means for the general model (Hayman, 1955,1958) are showed in Table 3.

Table 3. Coefficients for the components of the generation mean model

Generation	Components					
	m	[a]	[d]	[aa]	[ad]	[dd]
P	1	1	-1/2	1	-1	1/4
P' [a]	1	-1	-1/2	1	1	1/4
F_1	1	0	1/2	0	0	1/4
F_2	1	0	0	0	0	0
F_3	1	0	-1/4	0	0	1/16
B	1	1/2	0	1/4	0	0
B'	1	-1/2	0	1/4	0	0
BS	1	1/2	-1/4	1/4	-1/4	1/16
BS'	1	-1/2	-1/4	1/4	1/4	1/16

[a] P' refers to parent with lower mean value.

If epistasis is present, estimates of additive and dominance effects may be biased by epistasis and linkage disequilibrium and they are uninterpretable. Estimates of epistasis from a digenic model are unbiased if linkage of interacting loci and higher orders of epistasis are absent. While failure to fit the non-epistatic model is a definite indication of epistasis, failure to fit the digenic epistatic model may indicate either trigenic epistasis or linkage or both. The six-

parameter model provides an exact fit of the generation means and does not allow for the application of a goodness-of-fit test because all the degrees of freedom are used in the estimation of the six-parameters. Therefore, when an estimate of a parameter is either zero or its standard error is greater than its effect, it can be eliminated in the digenic epistatic model to provide at least one degree of freedom for making a goodness-of-fit test of the model. The significance of a parameter was tested by calculating a t value as the ratio between the estimated value of the parameter and its standard error.

Hayman's model provides a clear procedure for estimating the gene action, if the following assumptions apply:

a. two alleles per locus,
b. most positive alleles occur in one parent and most negative ones in the other,
c. no linkage of interacting loci (loci with epistatic effects),
d. environmental effects and genotypic effects are additive,
e. no trigenic or higher order epistasis.

Heterosis (Falconer, 1960) or heterobeltiosis (Fonseca and Patterson, 1968) was estimated by comparing F_1 and F_2 means with parental means.

Number of effective factor pairs

Data from the field experiment that contained F_2-derived and parental lines were used to estimate the numbers of effective factor pairs controlling the various traits. The number of independently segregating effective factor pairs was estimated by using the Castle-Wright formula (Castle and Wright, 1921). This formula is as follows:

$$n = \frac{(\bar{P} - \bar{P}')^2}{8(\sigma^2_{F_2} - \sigma^2_{F_1})} = \frac{(\bar{P} - \bar{P}')^2}{4\sigma^2_A}$$

where:

n = number of loci by which the parents in a cross carry different alleles,

$\bar{P}$ = mean value of higher parent,

$\bar{P}'$ = mean value of lower parent,

σ^2_A = additive genetic variance.

This formula will furnish an unbiased estimate of the number of loci if the following assumptions are fulfilled:

a. all segregating loci contribute equally to the trait,

b. no linkage exists among loci affecting the trait,

c. either no dominance occurs or the degree and direction of dominance of plus factors is similar for all loci,

d. all plus factors are contributed by one parent and all minus factors are contributed by the other parent,

e. no epistasis occurs among alleles at contributing loci, and

f. environmental and genotypic variances are independent and combine additively to give total variability.

If assumption d is not met, n will be underestimated because the value in the numerator of the formula will be too small. If this assumption is in question, it is better to use the range between the extreme F_2-line phenotypes (R) instead of the parental range (Weber, 1948, and Lawrence, 1974).

In my study, the genetic component of variance among F_2-derived lines in F_3 may have contained some non-additive genetic variance, and hence, eight times this component could overestimate $4\sigma^2_A$, hence the formula I will use to estimate the minimum number of effective factors is finally represented as:

$$n = \frac{R^2}{8\ \sigma_g^2}$$

The number of favorable factors affecting a trait in a cross that was contributed by each parent was estimated by using the procedure of Lawrence and Frey (1976), which is an extension of Castle-Wright formula.

The number of favorable factors in lower parents was calculated as follows:

$$n' = \frac{(\bar{X}_S - \bar{X}_{\bar{P}}) + (\bar{X}_{\bar{P}'} - \bar{X}_L)}{2} \quad \frac{(n)}{R}$$

where:

n' = number of favorable factors contributed by the lower parent,

$\bar{X}_S$ = mean of highest line,

$\bar{X}_{\bar{P}}$ = mean of higher parent,

$\bar{X}_{\bar{P}'}$ = mean of lower parent,

$\bar{X}_L$ = mean of lowest line,

(n) = number of effective factors,

R = range of F_2.

The number of favorable factors in the higher parent was obtained by subtraction, and because the number of factors estimate was a minimum, the number was approximated to the next largest integer.

The procedure described by Lawrence and Frey (1976) assumed that the highest line in the segregating F_2 contained more favorable factors than the higher parent because it obtained additional favorable factors from the lower parent, and similarly, the lowest line contains more unfavorable factors than the lower parent it obtained unfavorable factors from the higher parent.

Graphic representations of frequency distribution of the original data for all traits measured on F_2-derived lines from

the six crosses were used to verify the estimates obtained by the Castle-Wright formula, and also to determine the relative number of transgressive segregates.

Correlation analyses

Correlation coefficients were computed from components of variances and covariances obtained as indicated in Tables 4a and 4b, in the same way as Mode and Robinson (1959). The phenotypic correlations were computed as follow:

$$r_p = \frac{G_{XY}}{[G_{XX}\ G_{YY}]^{\frac{1}{2}}} \quad \frac{\sigma_{XY} + r\ \sigma_{G_XG_Y}}{[(\ \sigma^2_{e_X} + r\ \sigma^2_{G_X}\ )\ (\ \sigma^2_{e_Y} + r\sigma^2_{G_Y}\ )]^{\frac{1}{2}}}$$

where:

$\sigma_{XY} + r\ \sigma_{G_XG_Y}$ = total covariance between traits X and Y,

$\sigma^2_{e_X} + r\ \sigma^2_{G_X}$ = total variance of trait X,

$\sigma^2_{e_Y} + r\ \sigma^2_{G_Y}$ = total variance of trait Y.

Table 4a. Analysis of variance and covariance

Sources of variation	Degrees of freedom	Mean squares or mean cross product		
		XX	XY	YY
Entries	59	G_{XX}	G_{XY}	G_{YY}
Error	118	E_{XX}	E_{XY}	E_{YY}

Table 4b. Analysis of covariance and expectation of mean cross products

Sources of variation	Degrees of freedom	Mean cross product	Expected mean products
Entries	59	MP_1	$\sigma_{XY} + r\ \sigma_{G_XG_Y}$
Error	118	MP_2	σ_{XY}

The genotypic correlations were computed as follow:

$$r_A = \frac{\sigma_{G_XG_Y}}{(\ \sigma^2_{G_X}\ \ \sigma^2_{G_Y}\ )^{\frac{1}{2}}}$$

where:

$\sigma_{G_XG_Y}$ = genetic covariance between traits X and Y,

$\sigma^2_{G_X}$ = genetic variance of X trait,

$\sigma^2_{G_Y}$ = genetic variance of Y trait.

Significance of phenotypic correlation coefficients was determined by comparison to tabulated "r's" from Table A11 of Snedecor and Cochran (1963) using (n-2) degrees of freedom.

Coefficients of variation computed for all characters in each experiment are presented in Tables 26 and 28. They provided indications of the precision of measurements in the experiments.

EXPERIMENTAL RESULTS

My experimental results will be presented under five categories: (a) generation means analyses, (b) heterosis, (c) number of effective factor pairs, (d) transgressive segregation, and (e) correlation analyses.

Generation Means Analyses

Analyses of variance for testing variation among the generation means for each barley cross were performed on the original data from the controlled-environment and field experiments, and the results of the F tests from these analyses are presented in tables 5 and 6, respectively. In the controlled-environment chamber there were few cases of significant variation among generation means (Table 5), whereas in the field experiments half or more of the crosses showed significant variation among generation means when all traits were considered (Table 6). Heading date showed significant variation among generation means in all crosses in the field and seven of twelve in the controlled-environment experiment. For plant height, there was significance among means in ten crosses in the field and five in the controlled-environment experiment. Grain yield had no instance of significant variation among generation means in the controlled-environment experiment, but there were six crosses with significance for this trait in the

Table 5. Degrees of significance among generation means (according to F tests) for six traits measured in the controlled-environment chamber experiment

Cross number	Trait[a]					
	Heading date	Plant height	Grain yield	Straw yield	Harvest index	Number of panicles
1	**	*	ns	ns	ns	ns
2	ns	ns	ns	*	ns	*
3	*	ns	ns	ns	ns	ns
4	ns	ns	ns	ns	*	ns
5	ns	ns	ns	ns	ns	ns
6	ns	ns	ns	ns	ns	ns
7	*	*	ns	ns	ns	*
8	*	**	ns	*	ns	*
9	*	**	ns	ns	ns	ns
10	ns	ns	ns	ns	ns	ns
11	**	ns	ns	*	ns	ns
12	*	**	ns	ns	ns	ns

[a]ns, *, and ** denotes no significant variation among generation means and significant variation at the 5% and 1% levels of probability, respectively.

Table 6. Degrees of significance among generation means (according to F tests) for six traits measured in the field experiment

Cross number	Trait[a]					
	Heading date	Plant height	Grain yield	Bundle weight	Harvest index	300-seed weight
1	**	**	ns	**	**	**
2	**	**	ns	ns	**	**
3	**	**	ns	**	**	*
4	**	**	**	**	ns	**
5	**	*	ns	ns	ns	ns
6	**	ns	ns	ns	ns	ns
7	**	ns	**	*	**	**
8	**	**	**	**	**	**
9	**	**	ns	**	**	ns
10	**	*	**	**	ns	ns
11	**	**	**	**	*	**
12	**	**	*	*	ns	**

[a]ns, *, and ** denotes no significant variation among generation means and significant variation at the 5% and 1% levels of probability, respectively.

field. Of the six cases of significance for grain yield in the field, five were for interspecific crosses. For bundle weight, significance among generation means occurred for three crosses in the controlled-environment experiment, and for nine in the field. Only one cross showed significance for harvest index in the growth chamber, but seven showed significance in the field. Number of panicles gave significant variation among generation means for three crosses in the controlled-environment chamber and eight crosses showed significance for 300-seed weight.

In general, interspecific crosses showed a higher proportion of instances of significant variation among generation means than did the intraspecific ones. For example, in the field experiments, only 22 of 36 trait-cross cases showed significance among generation means for intraspecific crosses. Whereas 30 of 36 cases showed significance for interspecific crosses. And, of greatest importance for barley breeding was the fact that the greatest differences between inter and intraspecific crosses occurred for the vigor traits grain yield and bundle weight.

Of course, the Hayman procedure of generation-means analysis to estimate genetic effects could be applied only to those cross-trait cases that showed significant variation among generation means. Estimates of the various genetic components and the Chi-square for goodness-of-fit to the genetic

model are shown in Tables 7, 8 and 9 for the controlled-environment and field experiment, respectively.

In all instances except plant height in cross 11 in the field experiment, the general non-epistatic or digenic epistatic model satisfactorily fitted the data as indicated by the non-significant Chi-square values. However, for some trait-cross instances, the estimates did not provide an explanation for the type of gene action involved because the estimates had very high standard errors. For example, of 19 trait-cross cases analyzed from the controlled-environment experiment, only seven, seven, and twelve of the additive, dominance and epistatic component estimates, respectively, were significant.

In the field experiments, there were few trends with respect to genetic effects for any trait or any cross. One trend, however, was for heading date to show significant estimates of the additive component, but some estimates of dominance and epistatic components for this trait were significant also. For the vigor traits, plant height, grain yield, and bundle weight, few of the component estimates were significant. The significant estimates for harvest index were predominantly for the additive component, whereas for 300-seed weight, many estimates of additive, dominance, and epistatic components were significant.

The significance of dominance effects for yield in cross 7 were meaningful whereas in cross 10 it seemed to be biased be-

Table 7. Estimates of genetic components from the generation-mean analyses for heading date, plant height, straw yield, number of panicles, and harvest index and χ^2 for goodness-of-fit for barley crosses evaluated in the controlled-environment experiment

Trait	Cross number	Components[a] m	[a]	[d]
Heading date	1	72.0 ± 0.5	3.7 ± 1.5	19.2 ± 5.0
	3	68.1 ± 0.4	8.6 ± 0.9*	1.2 ± 1.0
	7	58.8 ± 1.3	8.3 ± 2.2*	-5.7 ± 4.4
	8	59.2 ± 0.4	1.7 ± 0.7	-14.0 ± 1.2**
	9	52.6 ± 0.3	3.5 ± 0.2*	9.5 ± 1.5
	11	59.6 ± 3.6	3.1 ± 3.2	-36.1 ± 19.2
	12	56.9 ± 0.4	1.8 ± 1.0	-15.3 ± 0.5*
Plant height	1	96.5 ± 1.7	6.1 ± 2.8	---
	7	84.3 ± 1.4	10.3 ± 1.8**	1.7 ± 3.7
	8	86.5 ± 0.3	5.3 ± 0.2*	3.5 ± 1.4
	9	92.0 ± 0.2	7.0 ± 0.5*	12.8 ± 0.7*
	12	87.2 ± 0.3	3.9 ± 0.7	---
Straw yield	2	15.1 ± 0.1	---	-5.4 ± 0.3*
	8	8.7 ± 1.2	---	7.0 ± 5.1
	11	10.1 ± 0.0	3.4 ± 0.0**	---
Number of panicles	2	8.6 ± 0.5	0.6 ± 0.1	-9.0 ± 2.3
	7	6.5 ± 0.1	1.4 ± 0.2	3.4 ± 0.3*
	8	7.8 ± 0.0	0.6 ± 0.0	5.3 ± 0.0**
Harvest index	4	18.0 ± 0.3	0.4 ± 0.2	22.6 ± 1.4*

[a] m = F_2 mean, [a]= pooled additive effects, [d]= pooled dominance effects, [aa]= pooled interaction between additive effects, [ad]=pooled interaction between additive and dominance effects, and [dd]= pooled interaction between dominance effects.

[b] ns χ^2 values are not significant. * and ** denotes significance at the 5% and 1% level of probability, respectively.

Dashes denote that the component did not improve the fit to the model.

[aa]	[ad]	[dd]	χ^2 for goodness of fit.
22.0 ± 4.2	---	-38.4 ± 9.4	1.32 ns[b]
---	2.9 ± 1.1	-12.5 ± 2.5	0.03 ns
---	---	---	1.32 ns
---	---	---	0.19 ns
20.7 ± 1.5*	---	-13.3 ± 2.4	0.01 ns
-20.9 ± 18.4	0.6 ---	46.5 ± 29.0	1.31 ns
---	0.6 ± 1.1	-5.8 ± 1.9	0.04 ns
6.7 ± 4.4	-4.8 ± 5.4	-55.9 ± 7.0	2.23 ns
---	---	---	1.54 ns
-13.7 ± 1.3	---	-18.1 ± 2.0	0.01 ns
2.4 ± 0.5	-9.1 ± 0.6*	---	0.01 ns
-9.0 ± 0.8	-11.3 ± 0.9*	43.1 ± 0.0*	0.02 ns
-8.3 ± 0.3*	-2.2 ± 0.1*	5.5 ± 0.5	0.00 ns
6.2 ± 5.0	-3.8 ± 0.5	-11.6 ± 5.3	0.02 ns
-1.7 ± 0.0*	2.1 ± 0.0*	-5.6 ± 0.1**	0.00 ns
-11.1 ± 2.3	---	10.5 ± 2.3	0.12 ns
2.4 ± 0.0*	---	-10.6 ± 0.0**	0.00 ns
---	1.3 ± 0.2	4.1 ± 0.7	0.02 ns
20.0 ± 1.4	---	-17.1 ± 2.2	0.00 ns

Table 8. Estimates of the genetic components from the generation-means analyses for heading date, plant height, and grain yield and χ^2 for goodness-of-fit for barley crosses evaluated in the field experiment

Trait	Cross number	Components[a] m	[a]	[d]
Heading date	1	60.5 ± 0.4	4.6 ± 1.3	---
	2	61.2 ± 0.3	1.3 ± 0.2	-5.3 ± 2.1
	3	61.5 ± 0.1	6.7 ± 0.4*	-11.8 ± 0.8*
	4	60.0 ± 0.1	9.0 ± 0.6*	-4.4 ± 1.1
	5	59.3 ± 0.1	7.3 ± 0.2*	---
	6	62.0 ± 0.0	2.5 ± 0.1*	0.8 ± 0.1
	7	55.2 ± 0.2	9.6 ± 0.9*	-10.8 ± 1.1
	8	56.2 ± 0.0	3.9 ± 0.1**	3.2 ± 0.2*
	9	59.2 ± 0.1	3.0 ± 0.1*	5.5 ± 0.3*
	10[c]	56.0 ± 0.3	2.7 ± 0.9	3.1 ± 1.1
	11	62.6 ± 1.2	7.0 ± 4.2	50.2 ± 10.5
	12	58.6 ± 0.1	---	7.2 ± 0.8
Plant height	1	77.8 ± 0.0	---	11.2 ± 0.0**
	2	80.0 ± 0.1	5.1 ± 0.1**	11.7 ± 1.4
	3	79.5 ± 0.5	1.3 ± 0.4	34.1 ± 4.6
	4	76.2 ± 0.3	18.5 ± 1.9	23.3 ± 3.8
	5	77.8 ± 4.1	6.5 ± 6.4	21.2 ± 27.1
	8	72.7 ± 1.5	-7.2 ± 2.9	0.2 ± 7.4
	9	79.4 ± 0.2	-4.3 ± 1.4	33.4 ± 1.1*
	10[c]	76.5 ± 1.4	-0.6 ± 4.3	-2.8 ± 2.8
	11	61.6 ± 4.0	7.0 ± 2.7	-124.5 ± 34.8
	12	82.4 ± 0.0	12.1 ± 0.1**	-13.6 ± 0.2**
Grain yield	4	34.6 ± 1.7	26.0 ± 12.0	31.9 ± 10.7
	7	32.5 ± 0.8	2.8 ± 1.6	26.4 ± 3.9**
	8	28.6 ± 0.3	5.3 ± 0.0**	-14.3 ± 2.0
	10[c]	29.8 ± 1.3	-11.4 ± 4.4	17.7 ± 5.1*
	11	28.5 ± 0.7	5.9 ± 0.8	21.8 ± 7.1
	12	37.8 ± 1.5	3.8 ± 1.0	18.8 ± 10.5

[a] m= F_2 mean, [a]= pooled additive effects, [d]=pooled dominance effects, [aa]= pooled interaction between additive effects, [ad]= pooled interaction between additive and dominance effects, and [dd]= pooled interaction between dominance effects.

[b] ns χ^2 values are not significant. [c] Eight generations were used in this cross. * and ** denotes significance at the 5% and 1% level of probability, respectively. Dashes denote that the component did not improve the fit to the model.

[aa]	[ad]	[dd]	χ^2 for goodness of fit.
-9.7 ± 2.9	2.1 ± 1.5	52.8 ± 12.3	0.55 ns[b]
4.1 ± 0.8	---	-11.6 ± 5.9	0.11 ns
-3.4 ± 0.3	4.9 ± 0.4	---	0.05 ns
---	7.9 ± 0.6	2.8 ± 2.1	0.06 ns
1.3 ± 0.4	7.0 ± 0.3*	5.3 ± 1.8	0.02 ns
1.1 ± 0.0*	1.4 ± 0.1*	---	0.00 ns
-0.0 ± 0.5	6.0 ± 0.9	---	0.06 ns
6.7 ± 0.1**	1.8 ± 0.1*	---	0.00 ns
4.1 ± 0.1*	1.6 ± 0.2	---	0.00 ns
5.0 ± 1.1*	0.8 ± 1.0	-2.6 3.2	0.57 ns
---	6.0 ± 5.6	90.7 ± 23.1	3.11 ns
-1.8 ± 0.8	-2.0 ± 0.1*	31.9 ± 4.0	0.07 ns
-28.0 ± 0.0**	-0.8 ± 0.0*	128.0 ± 0.0**	0.00 ns
-28.6 ± 1.0*	---	107.7 ± 5.6*	0.01 ns
-15.0 ± 2.7	---	109.4 ± 17.4	0.29 ns
7.5 ± 1.8	13.3 ± 2.0	---	0.19 ns
---	5.3 ± 6.8	38.5 ± 41.4	3.79 ns
-6.4 ± 2.6	-16.3 ± 3.4	---	0.32 ns
15.1 ± 0.6*	-8.6 ± 1.5	---	0.08 ns
-2.6 ± 8.8	-2.6 ± 5.1	13.0 ± 8.8	3.87 ns
27.3 ± 14.8	---	-338.2 ± 111.1	3.91 *
-10.1 ± 0.1**	8.6 ± 0.1**	---	0.00 ns
5.6 ± 4.5	22.0 ± 12.2	---	0.64 ns
---	---	---	2.86 ns
-2.6 ± 1.3	---	-66.7 ± 6.9	0.00 ns
7.3 ± 3.7	-21.4 ± 5.5*	---	2.02 ns
-16.9 ± 5.2	---	66.4 ± 29.3	0.15 ns
15.1 ± 5.7	---	-81.7 ± 32.1	0.27 ns

Table 9. Estimates of the genetic components from the generation-means analyses for bundle weight, harvest index, and 300-seed weight and χ^2 for goodness-of-fit for barley crosses evaluated in the field experiment

Trait	Cross number	Components[a] m	[a]	[d]
Bundle weight	1	101.3 ± 1.9	50.6 ± 5.9	---
	3	99.3 ± 3.4	23.5 ± 8.1	33.4 ± 14.6
	4	83.5 ± 0.7	72.5 ± 3.5*	---
	7	93.5 ± 0.8	-10.2 ± 2.5	97.7 ± 6.8*
	8	78.6 ± 1.5	-16.3 ± 3.6	-48.5 ± 11.2
	9	63.2 ± 0.0	---	60.4 ± 60.9
	10[c]	74.4 ± 7.8	-20.8 ± 27.6	37.0 ± 29.1
	11	59.5 ± 0.2	21.9 ± 0.4*	-30.3 ± 2.7
	12	87.6 ± 0.8	15.9 ± 3.8	---
Harvest index	1	36.2 ± 3.2	5.3 ± 1.9	-26.9 ± 24.6
	2	36.6 ± 0.6	11.8 ± 0.6**	0.3 ± 3.9
	3	30.5 ± 1.9	14.2 ± 7.2	-39.9 ± 16.5
	7	35.3 ± 0.4	6.7 ± 0.2*	7.7 ± 3.4
	8	36.2 ± 0.5	-7.0 ± 2.1	12.1 ± 4.9
	9	35.4 ± 1.1	6.9 ± 0.5*	-16.9 ± 7.3
	11	47.8 ± 0.0	-3.4 ± 0.1*	60.0 ± 0.3**
300-seed weight	1	10.0 ± 0.6	7.5 ± 0.7*	-9.4 ± 3.4
	2	10.6 ± 0.0	1.2 ± 0.0**	4.0 ± 0.0**
	3	14.0 ± 0.7	0.1 ± 0.3	6.7 ± 5.7
	4	12.8 ± 0.0	1.0 ± 0.0*	4.0 ± 0.0**
	7	12.8 ± 0.3	0.5 ± 0.2	9.6 ± 2.1
	8	10.6 ± 0.7	-0.1 ± 1.7	4.2 ± 5.1
	11	8.6 ± 0.0	1.6 ± 0.0*	-20.8 ± 0.0**
	12	11.8 ± 0.0	0.5 ± 0.1	-5.7 ± 0.2*

[a]m= F_2 mean, [a]= pooled additive effects, [d]= pooled dominance effects, [aa]= pooled interaction between additive effects, [ad]= pooled interaction between additive and dominance effects, and [dd]= pooled interaction between dominance effects.

[b]ns χ^2 values are not significant.

[c]Eight generations were used in this cross.

* and ** denotes significance at the 5% and 1% level of probability, respectively.

[aa]	[ad]	[dd]	χ^2 for goodness of fit.
33.2 ± 9.0	42.1 ± 6.4	23.6 ± 41.6	0.16 ns[b]
-19.0 ± 4.3	19.3 ± 8.4	---	0.13 ns
43.9 ± 4.1	54.3 ± 3.6*	-302.9 ± 18.1*	0.02 ns
---	-25.3 ± 3.0	75.4 ± 13.3	0.03 ns
---	-46.5 ± 3.7*	-196.3 ± 17.9	0.03 ns
-78.6 ± 36.9	-23.9 ± 3.6	475.2 ±191.2	0.82 ns
21.8 ± 28.2	-41.1 ± 29.0	-23.6 ± 84.0	5.26 ns
-54.5 ± 3.4*	---	101.4 ± 15.9	0.01 ns
26.6 ± 4.5	5.9 ± 4.1	-214.9 ± 20.0*	0.04 ns
31.6 ± 13.7	---	-165.1 ± 81.9	2.92 ns
10.5 ± 1.8	---	-18.1 ± 10.2	0.02 ns
---	7.8 ± 7.5	-51.3 ± 29.8	2.03 ns
-15.2 ± 1.8	---	64.2 ± 11.2	0.04 ns
---	-18.4 ± 2.4	30.6 ± 10.0	0.69 ns
-2.7 ± 4.4	---	-22.9 ± 23.1	0.15 ns
---	-11.2 ± 0.2*	94.6 ± 0.8**	0.00 ns
-3.7 ± 1.1	7.0 ± 0.7	---	0.84 ns
-1.6 ± 0.0**	---	12.8 ± 0.0**	0.00 ns
-2.0 ± 3.2	---	14.0 ± 19.5	2.96 ns
2.0 ± 0.0**	---	-3.2 ± 0.0**	0.00 ns
3.7 ± 1.3	---	-3.1 ± 6.9	0.57 ns
---	-1.5 ± 2.0	7.5 ± 9.1	2.84 ns
7.2 ± 0.0**	---	-64.0 ± 0.0**	0.00 ns
-2.5 ± 0.1*	-0.6 ± 0.1	---	0.00 ns

cause of the presence of significant epistatic effects. In cross 8, additive effects were highly significant and no significant epistatic effect was detected. When significant additive and dominance effects are detected with epistatic effects, the significance of the epistatic estimates are of primary interest because additive and dominance effects are confounded. Epistatic genes of a complementary nature governed the inheritance of 300-seed weight in crosses 2 and 11, harvest index in cross 11, and plant height in cross 1. Epistatic genes of a duplicate nature governed the inheritance of number of panicles in cross 8, and 300-seed weight in cross 4.

From the generation-means analyses, it was not possible to show any difference between intra and interspecific barley crosses for the type of gene action responsible for determining any trait.

Heterosis

I compared the F_1 values with their respective mid-parent and higher or lower parent values to evaluate the magnitude of heterosis and heterobeltiosis, respectively, in the controlled-environment experiment (Table 10). The F_1 generation was not evaluated in the field experiments (except in cross 10), so degrees of heterosis and/or heterobeltiosis expressed by the barley crosses could not be estimated directly.

Table 10. Generation means for traits measured on inter and intraspecific crosses of barley in the controlled-environment chamber

Trait	Cross number	Generations					
		P	P′ [a]	F_1	F_2	B	B′ [b]
Heading date	1	68.5	59.2	63.0	62.0	70.7	64.7
	2	68.5	62.0	63.8	65.0	69.5	64.0
	3	68.5	58.7	62.8	63.0	72.7	64.1
	4	62.0	60.0	54.9	60.5	63.0	57.6
	5	60.0	58.7	57.0	57.5	61.0	58.2
	6	67.8	59.2	62.9	64.3	65.4	64.0
	7	68.5	54.0	54.5	56.8	66.8	56.0
	8	69.5	68.5	54.0[c]	58.2	60.0	59.7
	9	68.5	61.8	54.0[c]	56.2	59.8	55.9
	10	60.0	54.0	55.3	56.2	56.0	55.0
	11	69.5	67.8	53.2[c]	59.6	58.7	50.9
	12	67.8	61.8	49.1[c]	56.3	58.0	56.3
Plant height	1	80.9	70.2	80.3	93.0	91.3	76.0
	2	70.3	70.2	77.9	72.0	73.0	71.2
	3	72.2	70.2	85.2	74.0	71.9	69.0
	4	80.5	70.3	78.0	75.8	79.7	75.0
	5	80.5	72.2	83.1	76.5	80.3	70.1
	6	80.9	65.2	74.6	74.0	75.1	68.5
	7	94.1	70.2	82.6	82.3	94.3	74.0
	8	70.2	61.1	82.7[c]	80.5	85.6	80.6
	9	104.0	71.9	98.3	91.9	96.3	89.3
	10	94.1	80.5	89.7	88.0	90.6	83.0
	11	65.2	61.1	76.8	71.5	66.0	61.0
	12	104.0	65.2	98.1	86.8	97.1	73.2

[a] P′ refers to parent with lower mean value.

[b] B′ refers to first backcross to parent with lower mean value.

[c] Significantly different than higher or lower parent.

Table 10 (Continued)

Trait	Cross number	Generations					
		P	P' [a]	F_1	F_2	B	B' [b]
Grain yield	1	2.9	1.9	3.0	2.6	2.9	2.0
	2	2.6	1.9	3.4	3.2	2.2	2.1
	3	2.3	1.9	2.6	2.0	2.3	2.1
	4	2.6	2.3	3.3	2.5	2.5	2.4
	5	2.3	2.3	3.3	2.6	2.2	2.2
	6	2.9	1.3	2.5	2.3	2.9	1.2
	7	1.9	0.6	1.6	1.4	1.3	0.6
	8	1.9	1.1	1.5	1.5	1.8	1.0
	9	1.9	0.8	1.2	1.0	1.8	0.9
	10	2.3	0.6	1.9	1.6	1.9	1.3
	11	1.3	1.1	2.0	1.9	1.4	1.2
	12	1.3	0.8	1.3	1.2	1.1	0.9
Straw yield	1	13.0	10.5	12.0	11.3	14.6	13.6
	2	13.0	8.7	13.8	14.1	13.1	13.0
	3	13.0	11.3	13.2	11.8	15.5	14.3
	4	9.1	8.6	12.1	11.8	10.4	9.4
	5	11.3	9.1	11.0	9.6	12.4	10.6
	6	10.5	8.3	9.3	9.6	11.8	10.1
	7	12.1	8.3	9.5	8.5	12.7	8.0
	8	13.0	5.7	9.3	8.7	10.4	10.1
	9	13.0	7.2	7.9	7.5	14.0	8.0
	10	9.1	8.3	8.4	8.3	8.3	7.5
	11	8.3	5.7	8.7	10.1	11.4	8.0
	12	8.3	7.2	8.0	7.0	7.4	7.3

Table 10 (Continued)

Trait	Cross number	Generations					
		P	P'[a]	F_1	F_2	B	B'[b]
Number of panicles	1	5.2	4.0	6.5	6.4	6.0	6.0
	2	5.2	4.0	6.7	8.6	6.3	5.3
	3	5.2	4.5	6.8	6.7	5.2	5.1
	4	4.5	4.0	4.8	4.7	4.8	4.8
	5	4.7	4.5	4.4	4.3	5.0	4.6
	6	4.0	3.2	3.8	3.7	4.1	3.9
	7	6.0	5.2	9.2[c]	6.4	7.3	5.8
	8	5.2	4.3	7.8[c]	7.8	8.7	8.1
	9	5.2	3.3	6.5	6.6	6.0	4.5
	10	6.0	5.8	5.8	5.9	7.8	7.4
	11	4.3	3.2	6.5	5.0	5.0	5.2
	12	5.3	3.3	5.3	5.0	5.2	4.5
Harvest index	1	18.0	15.0	19.0	18.0	19.5	17.0
	2	18.0	16.0	21.0	20.5	23.0	20.1
	3	18.0	15.3	17.0	17.0	20.0	20.0
	4	17.0	16.0	18.0	17.9	22.6	22.0
	5	17.0	15.3	17.0	16.8	17.5	16.8
	6	23.5	15.0	18.0	17.0	23.0	20.0
	7	18.0	13.8	23.0	18.0	23.0	20.0
	8	18.0	16.5	14.5	11.9	18.3	18.0
	9	21.0	18.0	24.5	24.0	21.0	18.6
	10	17.0	13.8	12.4	12.3	18.3	18.0
	11	23.5	16.5	22.0	21.0	28.0	19.0
	12	23.5	21.0	29.5	26.0	30.0	23.0

Table 11. Generation means for traits measured on inter and intraspecific crosses of barley in the field experiments

Trait	Cross number	Generations					
		P	P'[a]	F_2	F_3	BS	BS'[b]
Heading date	1	66.6	61.6	61.0[c]	63.8	63.8	59.4
	2	66.4	64.6	61.2[c]	61.8	63.2	62.2
	3	65.8	62.2	61.5[c]	64.4	65.8	61.6
	4	64.0	61.8	60.0[c]	61.2	64.0	58.8
	5	62.2	61.6	59.4[c]	59.6	61.8	58.0
	6	63.8	61.6	62.0	61.8	63.0	61.2
	7	64.2	57.0	55.2	58.0	61.0	54.4
	8	65.4	59.2	56.2[c]	55.4	58.6	55.6
	9	64.0	59.2	59.2[c]	57.8	60.0	57.8
	11	61.2	59.2	62.6[c]	54.4	58.2	54.2
	12	63.2	59.2	58.6[c]	58.8	59.0	57.8
Plant height	1	77.0	75.4	77.8	83.0	76.2	75.8
	2	77.6	67.4	80.0[c]	83.8	79.4	74.0
	3	76.0	73.6	79.5[c]	77.8	75.6	73.2
	4	77.2	66.8	76.2[c]	69.0	78.4	66.6
	5	78.0	75.6	77.8	77.2	76.6	71.4
	6	78.4	77.2	79.5	79.0	80.8	77.4
	7	80.4	77.4	87.2	77.2	75.6	75.2
	8	75.4	59.9	73.4[c]	73.0	71.0	70.0
	9	82.2	73.4	79.4	71.0	75.4	75.0
	11	74.0	59.4	61.6[c]	71.6	78.2	76.8
	12	82.6	75.6	82.4	85.8	87.2	79.4

[a] P' refers to parent with lower mean value.

[b] BS' refers to selfed generation of first backcross to parent with lower mean.

[c] Significant heterosis.

Table 11 (Continued)

Trait	Cross number	Generations					
		P	P'[a]	F_2	F_3	BS	BS'[b]
Grain yield	1	27.6	25.2	35.2	34.0	36.2	33.2
	2	31.3	22.8	38.4	32.0	33.5	22.6
	3	24.4	19.6	29.3	32.2	33.0	25.0
	4	34.5	21.6	34.4	26.0	38.8	23.0
	5	30.4	22.8	35.6	32.6	32.7	31.2
	6	29.6	28.0	30.6	27.2	37.6	27.6
	7	20.4	18.6	32.5[c]	28.0	27.8	22.0
	8	21.0	10.4	28.8[c]	28.2	30.0	25.0
	9	27.4	20.8	26.0	22.2	23.0	22.6
	11	30.2	11.4	28.5[c]	27.2	26.8	19.6
	12	30.6	25.0	37.8[c]	28.0	33.8	27.8
Bundle weight	1	82.5	65.4	96.0[c]	102.8	109.4	80.6
	2	71.2	56.3	100.0	91.8	76.8	70.2
	3	68.0	59.6	100.5[c]	91.2	92.4	75.4
	4	65.8	37.5	83.0[c]	64.6	98.2	54.4
	5	72.4	55.6	93.4	79.6	74.2	71.0
	6	60.0	59.4	75.0	67.8	76.8	71.2
	7	78.6	48.4	93.5[c]	75.4	74.8	72.4
	8	84.0	23.6	78.6	77.0	82.4	75.4
	9	98.2	48.6	63.2	77.8	62.0	57.0
	11	68.0	23.6	59.5	73.4	70.4	49.0
	12	70.6	50.8	88.2[c]	73.0	87.0	74.2

Table 11 (Continued)

Trait	Cross number	Generations					
		P	P' [a]	F_2	F_3	BS	BS' [b]
Harvest index	1	44.8	30.5	36.2	32.6	45.4	36.8
	2	46.2	30.6	36.6	35.4	44.0	31.6
	3	44.0	31.2	30.5	35.2	43.8	32.8
	4	50.3	45.0	47.0	43.0	47.8	38.8
	5	42.2	42.0	40.0	39.0	41.6	39.5
	6	46.6	40.0	41.0	42.0	49.0	48.4
	7	41.0	25.8	35.3	37.4	37.2	30.0
	8	49.2	26.4	36.2	36.2	36.0	33.8
	9	42.6	28.2	35.4	38.2	40.8	34.8
	11	49.2	39.6	47.8	38.6	39.8	37.6
	12	39.4	35.4	42.8	36.0	37.6	36.6
300-seed weight	1	11.6	10.6	10.6	12.6	13.4	9.4
	2	11.4	9.0	10.6	10.4	10.6	9.4
	3	12.2	12.2	14.0[c]	13.2	13.0	11.8
	4	13.0	11.0	12.8	11.6	12.6	11.6
	5	11.6	11.2	11.6	11.6	11.8	11.0
	6	10.8	10.6	10.8	10.6	10.6	10.6
	7	11.2	10.4	12.8[c]	10.2	11.6	10.8
	8	11.8	9.0	10.6	10.6	10.0	9.6
	9	11.4	10.4	10.4	10.0	11.0	11.0
	11	11.8	8.6	8.6	9.8	12.4	10.8
	12	13.2	11.0	11.8	13.2	13.0	12.8

Table 12. Generation means for traits in cross 10 in the field experiment

Generation	Trait					
	Heading date	Plant height	Grain yield	Bundle weight	Harvest index	300-seed weight
P	60.8	82.2	36.0	96.8	42.0	10.8
P'[a]	57.0	74.6	18.6	48.4	35.4	10.4
F_1	56.8[b]	78.4	38.0[b]	87.4	43.0	11.4
F_2	56.2	78.4	31.6	77.6	41.2	11.2
F_3	55.4	76.2	23.8	58.0	41.0	11.2
B	58.6	72.6	24.8	83.4	39.4	11.2
BS	57.2	79.6	29.0	63.6	38.8	11.3
BS'	54.8	77.0	25.8	65.0	35.0	11.0

[a]'P' refers to parent with lower mean value.
[b]Significantly different than midparent value.

However, for the field experiments, I estimated heterosis or heterobeltiosis indirectly. I assumed that the F_2 mean (Tables 11 and 12) had regressed 50 percent from the F_1 value due to inbreeding. Therefore, the degree of heterosis expected in the F_1 generation, was estimated by doubling the difference between the F_2 mean and the midparent value.

Generally, heterosis was positive for the vigor traits, grain yield, plant height, and bundle weight, whereas heading date consistently showed negative heterosis, i.e., earlier

than the midparent values (Tables 13 and 14).

Heterosis for earliness in heading date tended to be significant for interspecific crosses in both the controlled-environment and field experiments; however, in the field, most intraspecific crosses also showed significant heterosis for this trait (Table 13). Three interspecific crosses, i.e., 8, 11, and 12, showed heterobeltiosis for heading date. Heading date was the trait that showed the highest incidence of crosses with significant heterosis. In both, field and controlled-environment experiments, the average and range of heterosis for heading date was slightly greater in inter than in intraspecific crosses (Table 16 and 17).

Heterosis for grain yield in the field experiment ranged from 13 percent in cross 6 to 167 percent in cross 8 and for bundle weight from 14 percent in cross 9 to 61 percent in cross 4 (Table 13). The frequencies of significant heterosis for grain yield were five of six crosses in the inter and none of six in intraspecific crosses, whereas for both bundle weight and plant height the frequencies of significant heterosis were three and two crosses, respectively. The average levels of heterosis for grain yield was 84 and 57 percent in inter and intraspecific crosses, respectively (Table 16). However, for bundle weight, the average degrees of heterosis were similar for intra and interspecific crosses (i.e., 44 vs 34 percent, respectively). The average levels of heterosis

Table 13. Percentage of heterosis for heading date, plant height, and grain yield for intra and interspecific barley crosses evaluated in the controlled-environment and field experiments

Trait	Cross number	Percentage of heterosis	
		Controlled-environment experiment	Field experiment
Heading date	1	-1.4	-9.7[a]
	2	-2.3	-13.1[a]
	3	-1.9	-7.8[a]
	4	-10.0	-9.2[a]
	5	-4.0	-8.1[a]
	6	-1.0	-2.2
	7	-11.1	-17.8
	8	-21.7[a]	-19.6[a]
	9	-17.0[a]	-7.8[a]
	10	-3.0	-3.6[a]
	11	-22.5[a]	8.0[a]
	12	-16.2[a]	-8.4[a]
Plant height	1	6.3	4.2
	2	10.9	20.6[a]
	3	20.3	12.6[a]
	4	2.6	11.6[a]
	5	8.8	13.6
	6	2.2	5.1
	7	0.6	21.1
	8	25.9[a]	17.0[a]
	9	11.8	4.2
	10	2.8	0.0
	11	21.7	15.2[a]
	12	10.5	8.4
Grain yield	1	22.9	66.7
	2	59.3	84.5
	3	27.6	66.4
	4	34.8	45.2
	5	45.4	67.7
	6	18.3	12.5
	7	31.7	134.4[a]
	8	39.5	166.6[a]
	9	12.7	15.8
	10	27.6	39.0[a]
	11	63.1	74.0[a]
	12	24.3	72.0[a]

[a]Significant heterosis.

Table 14. Percentage of heterosis for straw yield and harvest index for intra and interspecific barley crosses evaluated in the controlled-environment and field experiments

Trait	Cross number	Percentage of Heterosis: Controlled-environment experiment	Percentage of Heterosis: Field experiment
Straw yield or Bundle weight	1	2.1	29.8[a]
	2	27.2	46.3
	3	8.6	57.5[a]
	4	36.7	60.7[a]
	5	7.8	42.6
	6	-1.1	27.6
	7	-6.9	47.3[a]
	8	-0.5	46.1
	9	-21.8	13.9
	10	-3.4	20.4
	11	-24.3	29.9
	12	-3.2	45.3[a]
Harvest index	1	15.2	-3.8
	2	23.5	-4.7
	3	2.1	-18.9
	4	9.1	-1.4
	5	5.3	-5.0
	6	-6.5	-5.3
	7	44.7	5.7
	8	-15.9	-4.2
	9	25.6	0.0
	10	-19.5	11.1
	11	10.0	7.7
	12	32.6	14.4

[a]Significant heterosis.

Table 15. Percentage of heterosis for 300-seed weight and number of panicles for intra and interspecific barley crosses evaluated in the controlled-environment and field experiments

Trait	Cross number	Percentage of Heterosis: Controlled-environment experiment	Percentage of Heterosis: Field experiment
300-seed weight	1	---	-9.0
	2	---	7.8
	3	---	29.5[a]
	4	---	13.3
	5	---	3.5
	6	---	1.9
	7	---	37.0[a]
	8	---	3.8
	9	---	-9.2
	10	---	7.5
	11	---	-31.4
	12	---	-5.0
Number of panicles	1	41.3	---
	2	45.7	---
	3	40.2	---
	4	12.9	---
	5	-4.3	---
	6	5.6	---
	7	64.3[a]	---
	8	64.2[a]	---
	9	52.9	---
	10	-1.7	---
	11	73.3	---
	12	23.3	---

[a]Significant heterosis.

Table 16. Means and ranges of heterosis percentages for intra and interspecific crosses of barley evaluated in field experiments

	Type of cross	Trait					
		Heading date	Plant height	Grain yield	Bundle weight	Harvest index	300-seed weight
Average percentage of heterosis	Interspecific	12	11	84	34	6	8
	Intraspecific	8	11	57	44	7	1
Range (%)	Interspecific	4-20	0-21	16-167	14-47	0-14	4-37
	Intraspecific	2-13	4-21	13- 85	28-61	1-19	2-30
Percent of significant cases	Intraspecific	83	33	83	33	0	17
	Intraspecific	83	50	0	50	0	17

Table 17. Means and ranges of heterosis percentages for intra and interspecific crosses of barley evaluated in controlled-environment experiments

	Type of cross	Trait					
		Heading date	Plant height	Grain yield	Straw yield	Harvest index	number of panicles
Average percentage of heterosis	Interspecific	15	12	33	1	13	46
	Intraspecific	3	9	35	27	8	48
Range (%)	Interspecific	3-23	1-26	13-63	1-24	10-45	24-73
	Intraspecific	1-10	2-20	18-59	2-37	2-24	6-46
Percent of significant cases	Interspecific	67	17	0	0	0	33
	Intraspecific	0	0	0	0	0	0

for plant height in the field experiments, however, were 11 percent for both intra and interspecific crosses. For 300-seed weight, there was significant and positive heterosis in one intra and one interspecific cross (Table 15). Also, there was significant heterosis or heterobeltiosis for number of panicles in two interspecific crosses in the controlled-environment experiment. (Table 15). No case of significant heterosis was found for harvest index (Table 14). In general, the average, range, and percentage of significant cases of heterosis were greater for grain yield, the most important trait, in inter than in intraspecific crosses in field experiments (Table 16).

Number of Effective Factor Pairs

Generally, the minimum numbers of segregating loci for grain yield and bundle weight were larger than the number for heading date, plant height and harvest index (Table 18). The minimum number of effective factor pairs segregating for grain yield and bundle weight was about 6.0, whereas the minimum number for heading date and plant height was about 3.0, and for harvest index about 4.0. For all traits except grain yield in cross 7, the estimated number of effective factor pairs were less than the haploid chromosome number, i.e., seven, for Hordeum. Generally, the mean minimum numbers of effective factor pairs for any trait was

Table 18. Parental ranges, progeny ranges, genetic variances, and estimated number of effective factors segregating for heading date, plant height, bundle weight, grain yield and harvest index in six barley crosses

Trait	Cross number	Parental range (P-P')	Progeny range (R)	Genetic variance (σ^2_g)	Number of effective factors (n) and average over type of cross	
Heading date	2	1.1	14.7	9.1	3.0	
	4	3.4	14.0	5.7	4.3	$\bar{X}_n^a = 4.1$
	5	0.1	18.3	8.3	5.0	
	7	9.1	15.7	10.7	2.9	
	8	7.6	13.3	14.3	1.5	$\bar{X}_n^b = 2.9$
	12	4.4	13.6	7.1	3.3	
Plant height	2	11.1	27.3	25.6	3.6	
	4	12.0	27.0	35.0	2.6	$\bar{X}_n = 3.0$
	5	3.8	26.0	31.3	2.7	
	7	3.4	28.7	36.4	2.8	
	8	14.1	36.3	40.8	4.0	$\bar{X}_n = 3.1$
	12	9.1	22.7	24.6	2.6	
Bundle weight	2	18.6	86.0	170.3	5.4	
	4	35.1	88.7	197.3	5.0	$\bar{X}_n = 5.5$
	5	23.3	77.3	124.4	6.0	
	7	35.4	77.3	123.9	6.0	
	8	53.6	67.0	114.5	4.9	$\bar{X}_n = 5.5$
	12	22.9	64.3	93.8	5.5	
Grain yield	2	2.8	41.0	45.5	4.6	
	4	13.9	45.0	37.7	6.7	$\bar{X}_n = 5.9$
	5	8.4	41.0	33.0	6.4	
	7	4.0	28.7	12.5	8.2	
	8	12.0	33.0	23.4	5.8	$\bar{X}_n = 6.1$
	12	7.1	30.0	27.0	4.2	
Harvest index	2	16.7	40.3	47.1	4.3	
	4	2.1	34.7	38.2	3.9	$\bar{X}_n = 4.0$
	5	2.1	29.0	28.6	3.7	
	7	17.9	23.7	21.1	3.3	
	8	19.2	23.7	15.8	4.4	$\bar{X}_n = 3.5$
	12	4.9	18.4	15.0	2.8	

[a]Intraspecific crosses.
[b]Interspecific crosses.

similar for inter and intraspecific crosses.

Frequency distributions for traits measured on F_2-derived lines in the intra and interspecific barley crosses are presented in figures 1 to 5. The frequency distributions for grain yield and bundle weight in the F_2 populations could not be grouped into sharp classes (Figs. 3 and 4). However, for heading date in crosses 2, 7, and 8, for plant height in crosses 4, 5, 7, and 12, and for harvest index in cross 12, six or seven rather well-defined classes could be distinguished; so, genetic analyses were performed to determine whether the modes of inheritance discriminated from the frequency distributions coincided with the estimates obtained from the Castle-Wright formula. The result of the genetic analysis for these eight trait-cross cases are presented in Table 19 and 20. For example, in cross 2, I estimated that there were three segregating factor pairs for heading date. On the assumption that two of them showed dominance for earliness, the Chi-square test showed a satisfactory fit for the three-factor hypothesis. Cross 7 for heading date and cross 12 for plant height showed satisfactory fit to a three factor pairs hypothesis with equal contributions and no dominance. Plant height in crosses 4, 5, and 7, gave satisfactory fits to the hypothesis of three segregating factor pairs with one of them showing dominance for tallness. However, for heading date in cross 8 and harvest index in cross

Table 19. Genetic analysis for heading date and harvest index in four barley crosses

Heading date									Harvest index		
Cross 2			Cross 7			Cross 8			Cross 12		
Mean	Obs.	Calc.	Mean	Obs.	Calc.	Mean	Obs.	Calc.	Mean	Obs.	Calc.
57.7	7	8	50.0	1	1	52.0	4	3	33.0	4	1
60.1	23	17	52.7	8	6	54.5	16	13	36.1	9	6
62.5	16	14	55.4	19	14	57.5	12	22	39.2	12	14
65.0	9	11	58.1	13	19	60.5	13	18	42.3	11	19
67.4	3	7	60.8	11	14	63.5	14	7	45.4	9	14
69.9	1	2	63.5	7	6	66.0	1	1	48.5	12	6
72.3	1	1	66.0	1	1	--	--	--	52.0	3	1
$\chi^2 = 5.68$ Prob. 50-25%			$\chi^2 = 5.16$ Prob. 75-50%			$\chi^2 = 13.9$ Prob. < 5%			$\chi^2 = 25.01$ Prob. < 5%		

Table 20. Genetic analysis for plant height in four barley crosses

Cross 4			Cross 5			Cross 7			Cross 12		
Mean	Obs.	Calc.	Mean	Obs.	Calc.	Mean	Obs.	Calc.	Mean	Obs.	Calc.
58.0	1	1	57.3	2	1	60.0	1	1	72.3	2	1
62.5	4	7	61.6	2	4	65.0	5	4	76.1	6	6
67.0	8	5	66.0	11	12	69.0	11	8	79.9	12	14
71.5	12	11	70.3	12	11	74.0	17	15	83.6	14	19
76.0	16	22	74.7	19	18	79.0	11	18	87.4	13	14
80.5	17	11	79.0	11	11	83.0	12	11	91.2	11	6
85.0	12	3	83.3	3	3	88.0	3	3	95.0	2	1
$\chi^2 = 5.24$ Prob. 75-50%			$\chi^2 = 2.23$ Prob. 90-75%			$\chi^2 = 4.46$ Prob. 75-50%			$\chi^2 = 7.85$ Prob. 25-10%		

12 the Chi-square values were significant, which suggested that the hypothesis of three segregating factor pairs controlling these instances was not true.

Means, standard deviations, and skewness and kurtosis values for the F_2 populations from the six barley crosses are given in Table 21. No skewness value showed significance which indicated that the F_2 populations fitted normal distributions. From a genetic standpoint, non-significance of skewness suggest either no dominance for factors conditioning a trait or no genes with major effect.

Transgressive Segregation

A primary objective of my study was to determine whether H. spontaneum would contribute genes, that when placed in a H. vulgare genotypic background, would make cultivated barley more desirable and/or productive. In other words, would transgressive segregation occur in a desired direction from interspecific crosses, and of more importance, would the frequency and level of transgression be more probable from inter than from intraspecific crosses.

The presence of transgressive segregation constitutes evidence for (a) multiple-factor control for a trait and (b) that the parents contribute different alleles toward expression of a trait. Of course, for transgressive segrega-

Table 21. Means, standard deviations, and skewness and kurtosis values for the frequency distributions of F_2-derived lines from six crosses

Trait	Cross number	Mean	Standard deviation	Skewness	g_1	kurtosis	g_2
Heading date	2	62.0	3.2	1.30	ns[a]	2.04	*
	4	62.1	2.6	0.74	ns	1.10	**
	5	62.1	3.1	-0.11	ns	1.32	**
	7	57.5	3.5	0.25	ns	-0.70	**
	8	58.6	3.9	0.05	ns	-1.33	**
	12	59.9	2.8	1.13	ns	1.17	**
Plant height	2	73.1	5.6	-0.60	ns	0.53	**
	4	74.4	6.5	-0.53	ns	-0.34	**
	5	72.5	6.0	-0.56	ns	0.04	**
	7	75.4	6.6	-0.04	ns	-0.54	**
	8	73.3	7.2	-0.57	ns	1.21	**
	12	84.5	5.5	-0.23	ns	-0.74	**
Grain yield	2	30.4	8.7	-0.09	ns	-0.33	**
	4	31.3	8.7	-0.20	ns	0.23	**
	5	29.8	8.8	-0.17	ns	0.31	**
	7	29.3	6.3	0.71	ns	0.50	**
	8	24.0	6.5	-0.15	ns	-0.15	**
	12	29.6	7.0	-0.09	ns	-0.40	**

[a]ns values are not significant.

* and ** denotes significance at the 5% and 1% level of probability, respectively.

Table 21 (Continued)

Trait	Cross number	Mean	Standard deviation	Skewness	g_1	kurtosis	g_2
Bundle weight	2	75.6	17.6	-0.20	ns	-0.24	**
	4	76.8	18.5	-0.02	ns	0.27	**
	5	72.7	17.7	-0.38	ns	-0.38	**
	7	71.6	15.8	0.63	ns	0.58	**
	8	57.5	14.4	-0.39	ns	0.42	**
	12	69.8	14.7	-0.48	ns	-0.25	**
Harvest index	2	40.5	7.7	-0.86	ns	1.57	**
	4	40.7	7.0	-0.81	ns	0.98	**
	5	40.7	6.4	0.61	ns	0.58	**
	7	41.2	5.5	-0.41	ns	-0.18	**
	8	41.8	5.0	-0.39	ns	0.01	**
	12	42.5	4.9	0.07	ns	-0.97	**

tion to occur, the effects of genes at different loci on the phenotype must be cumulative.

Means for the highest and lowest F_2-derived lines and the parents for heading date, plant height, bundle weight, grain yield, and harvest index for the six crosses are presented in Table 22. Extreme F_2-derived lines transcended the range of the parents for all traits except for low harvest index in crosses 7 and 8. According to my definition, a transgressive line had to exceed the parental mean by one least significant difference value. The numbers of such lines that fitted this definition of transgression for the various traits in the six barley crosses are presented in Table 23.

Transgressive F_2-derived lines occurred for all traits at least in one direction in all crosses except plant height in cross 4, bundle weight in cross 8, and harvest index in cross 7 and 8 (Table 23 and Figs. 1 to 5). Transgressive segregation for heading date occurred in all crosses and much more frequently for earliness than for lateness. The highest frequency of transgressive lines for heading date was found in intraspecific cross 2 where 26 lines were transgressive for earliness. For plant height there were no tall transgressive segregates in intraspecific crosses, whereas both tall and short transgressive segregates occurred in the interspecific crosses. There was no transgressive line for hight harvest index in any cross and 20 of 27 transgressive lines

Table 22. Highest and lowest F_2-derived lines and means of parents for heading date, plant height, bundle weight, grain yield and harvest index for six barley crosses evaluated in the field

Trait	Cross number	Highest line	Lowest line	Higher parent (P)	Lower parent (P')
Heading date	2	72.3	57.7	63.3	65.2
	4	70.0	56.0	65.2	61.8
	5	70.7	52.3	61.9	61.8
	7	65.7	50.0	66.3	57.3[a]
	8	65.3	52.0	66.3	58.7[a]
	12	69.3	55.7	64.0	59.6[a]
Plant height	2	83.0	55.7	76.9	65.8
	4	85.0	58.0	77.8	65.8
	5	83.3	57.3	77.8	73.9
	7	88.3	59.7	76.9	73.5[a]
	8	87.0	50.7	76.9	62.8[a]
	12	95.0	72.3	85.3[a]	76.2
Grain yield	2	50.3	9.3	23.7	20.9
	4	51.0	6.0	37.6	23.7
	5	49.0	8.0	37.6	29.2
	7	47.7	19.0	20.9	16.9[a]
	8	40.0	7.0	20.9	8.8[a]
	12	44.3	14.3	32.6	25.5[a]
Bundle weight	2	115.3	29.3	72.2	53.6
	4	121.3	32.7	88.6	53.6
	5	107.3	30.0	88.6	65.3
	7	117.7	40.3	72.2	36.8[a]
	8	85.0	18.0	72.2	18.6[a]
	12	96.0	31.7	76.5	53.6[a]
Harvest index	2	53.3	13.0	44.6	27.9
	4	52.0	17.3	44.6	42.5
	5	51.0	22.0	44.5	42.5
	7	51.7	28.0	45.8[a]	27.9
	8	52.3	28.7	47.1[a]	27.9
	12	51.7	33.3	47.7[a]	42.8

[a] *H. spontaneum* parent.

Table 23. Number of favorable genes contributed by the respective parents and the numbers of transgressive F_2-derived lines in the interspecific and intra specific crosses of barley

Trait	Cross number	Number of plus factors in parents		Transgressive lines	
		P	P' [a]	Higher than P	Lower than P' [a]
Heading date	2	2	2	2	26
	4	3	2	2	2
	5	3	3	4	5
	7	3	1[b]	0	2
	8	2	1[b]	0	9
	12	3	2[b]	1	2
Plant height	2	3	2	0	1
	4	2	1	0	0
	5	2	2	0	10
	7	2	2[b]	4	3
	8	3	2[b]	2	2
	12	2[b]	1	4	0
Grain yield	2	3	3	19	1
	4	5	3	1	1
	5	4	3	2	5
	7	5	4[b]	28	0
	8	4	2[b]	9	0
	12	3	2[b]	3	3
Bundle weight	2	5	1	5	1
	4	4	2	2	0
	5	4	3	0	5
	7	5	2[b]	6	0
	8	5	1[b]	0	0
	12	4	2[b]	1	1
Harvest index	2	3	2	0	1
	4	3	2	0	9
	5	2	2	0	10
	7	3[b]	1	0	0
	8	4[b]	1	0	0
	12	2[b]	1	0	7

[a] P' refers to parent with lower mean value.

[b] H. spontaneum parent.

Figure 1. Frequency distributions for heading dates (days after sowing) of F_2-derived lines from intra and interspecific crosses of barley evaluated in the field.

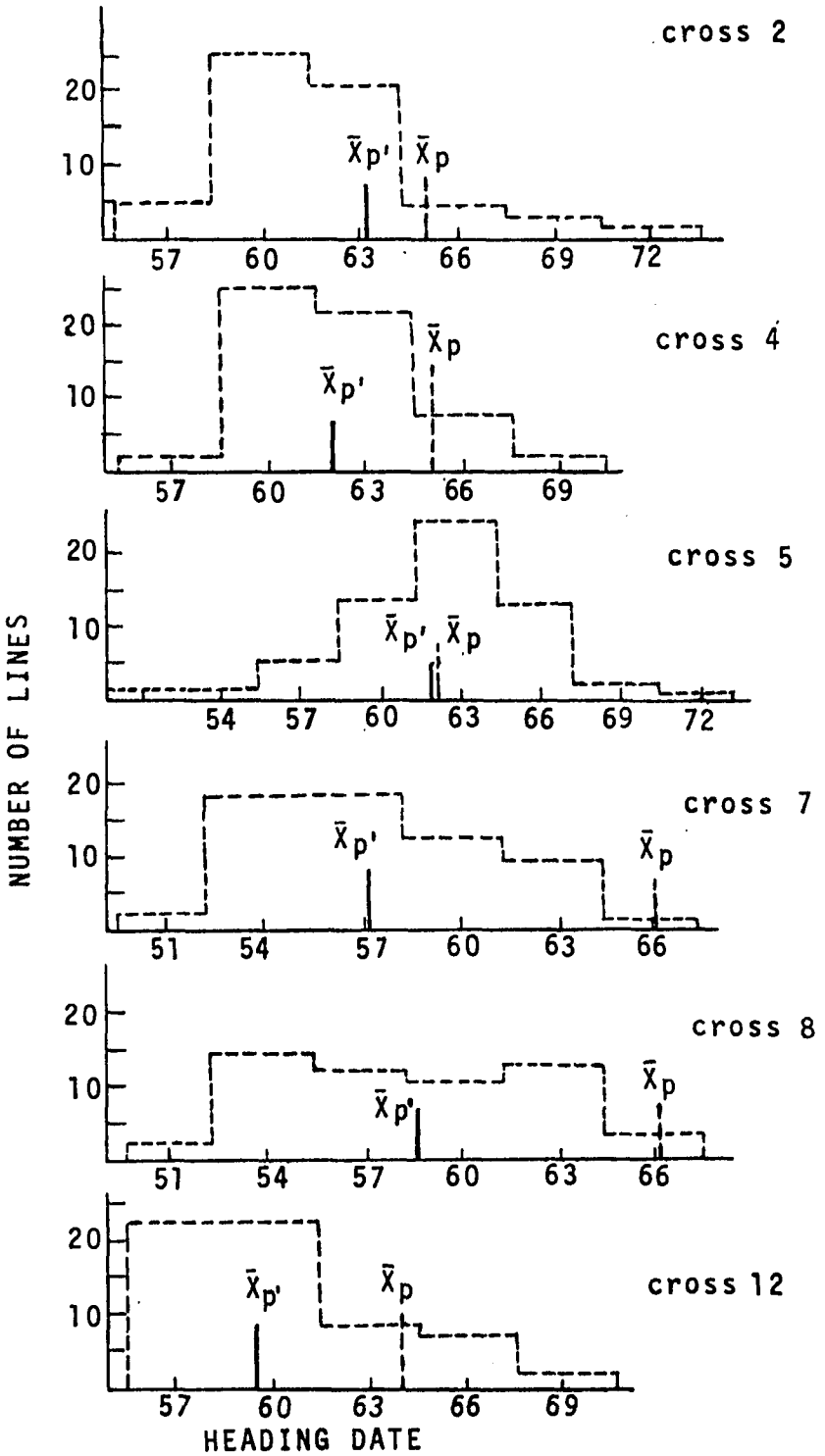

cross 2
cross 4
cross 5
cross 7
cross 8
cross 12
NUMBER OF LINES
HEADING DATE
$\bar{X}_{p'}$
$\bar{X}_p$
20
10
57
60
63
66
69
72
54
51

Figure 2. Frequency distributions for plant height (cm) of F_2-derived lines from intra and interspecific crosses of barley evaluated in the field.

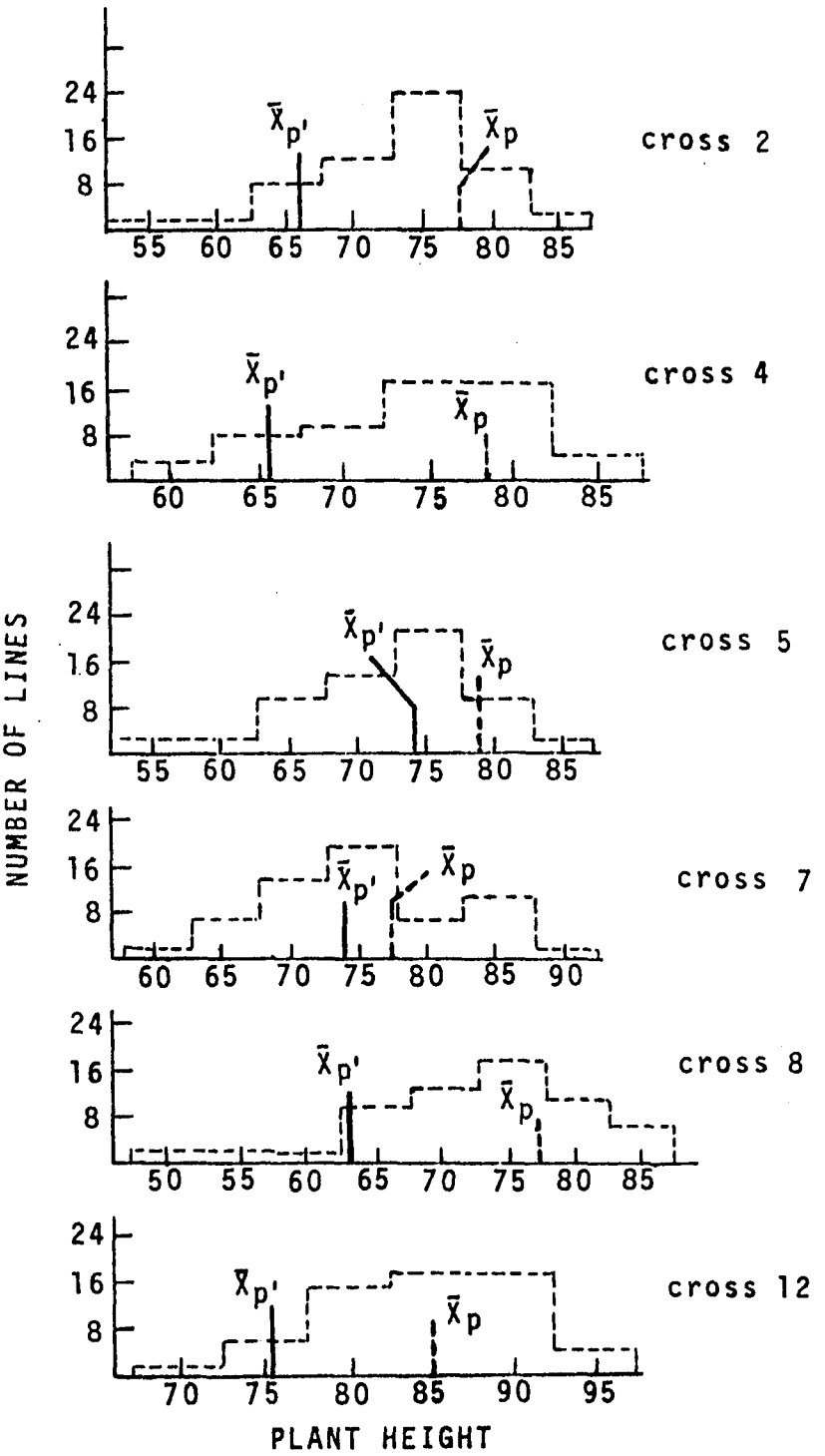

NUMBER OF LINES
24
16
8
$\bar{X}_{p'}$
$\bar{X}_p$
cross 2
55 60 65 70 75 80 85
cross 4
60 65 70 75 80 85
cross 5
55 60 65 70 75 80 85
cross 7
60 65 70 75 80 85 90
cross 8
50 55 60 65 70 75 80 85
cross 12
70 75 80 85 90 95
PLANT HEIGHT

Figure 3. Frequency distributions for grain yield (g/plot) of F_2-derived lines from intra and interspecific crosses of barley evaluated in the field.

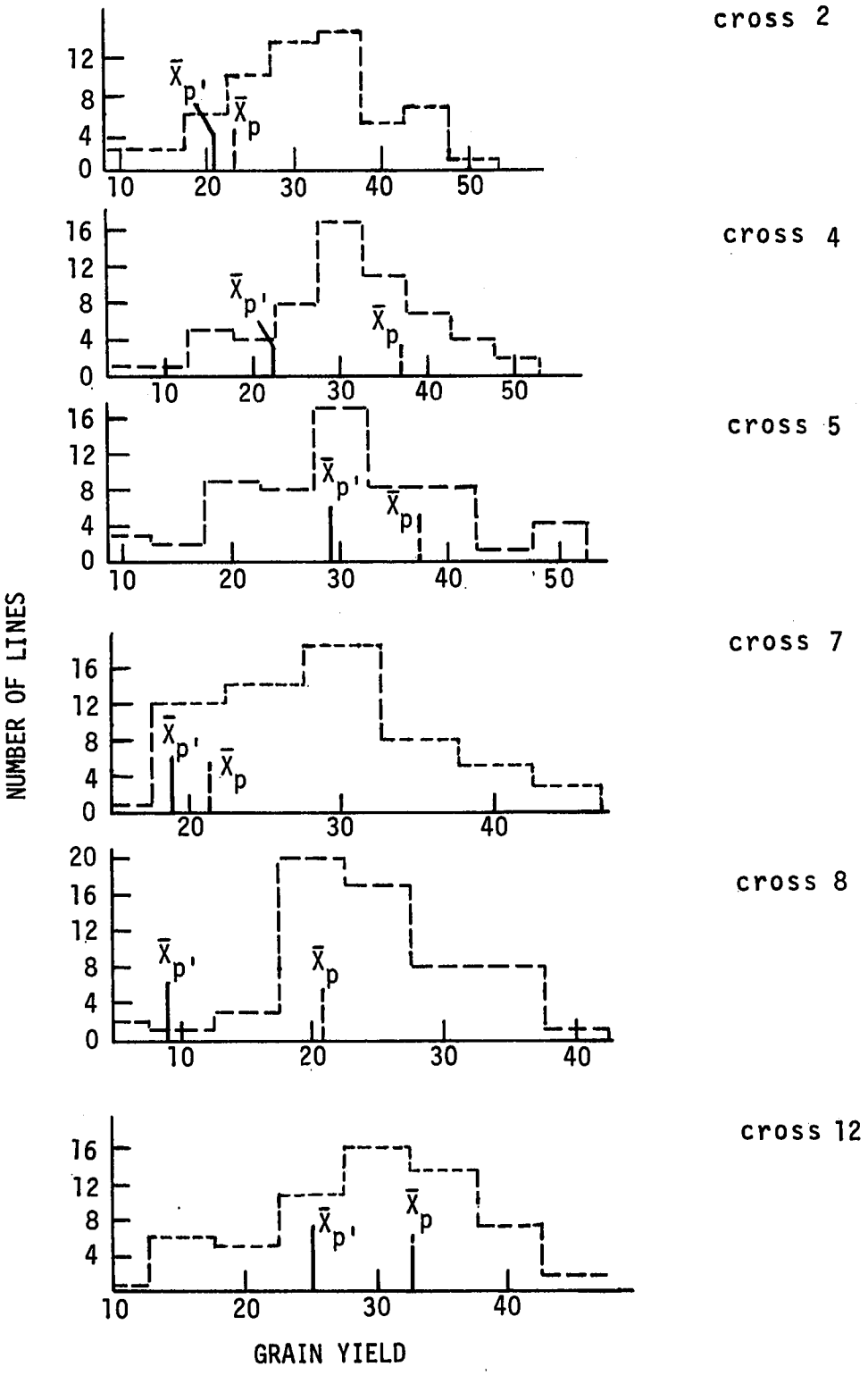

cross 2
cross 4
cross 5
cross 7
cross 8
cross 12
NUMBER OF LINES
GRAIN YIELD
$\bar{X}_{p'}$
$\bar{X}_p$

Figure 4. Frequency distributions for bundle weight (g/plot) of F_2-derived lines from intra and interspecific crosses of barley evaluated in the field.

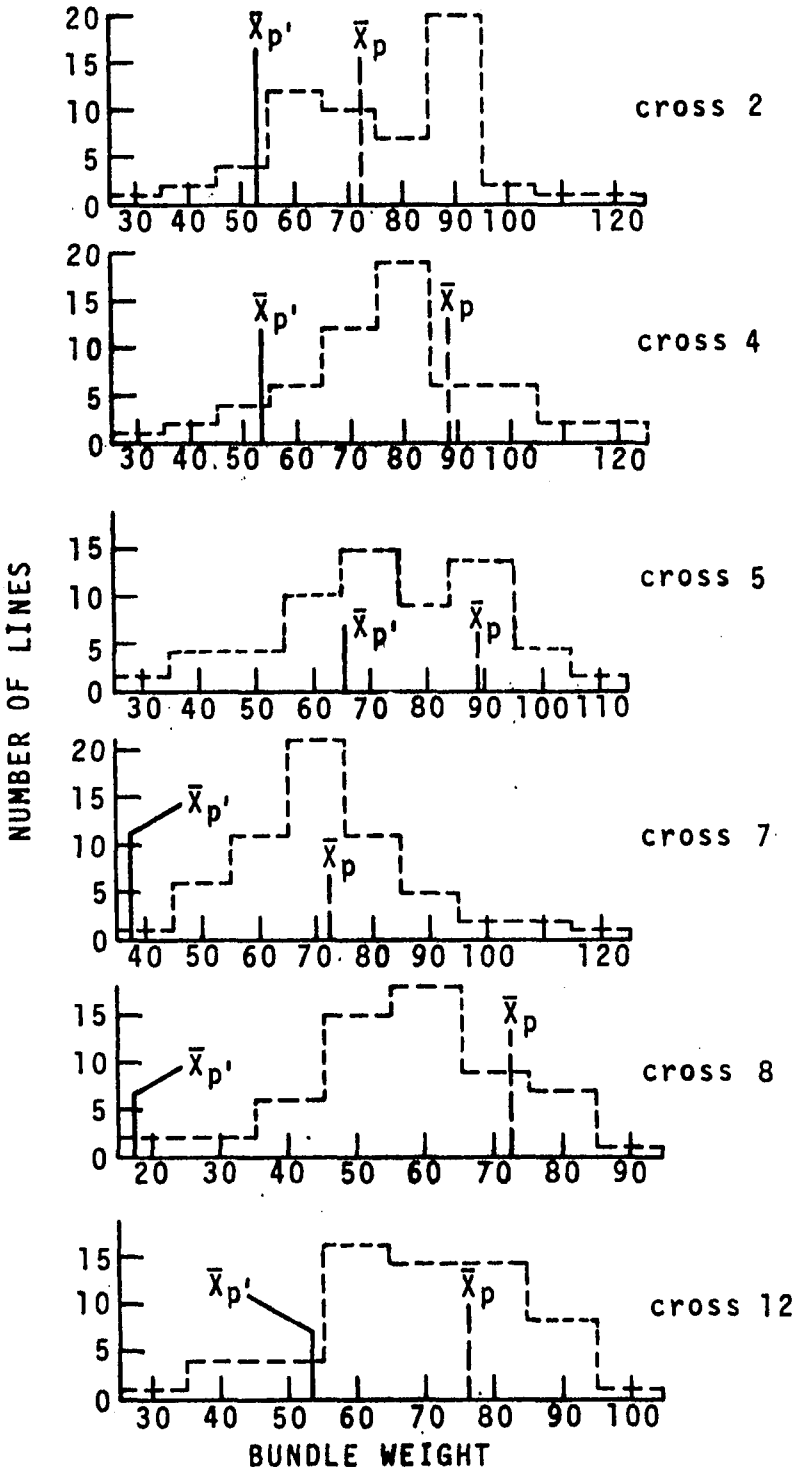
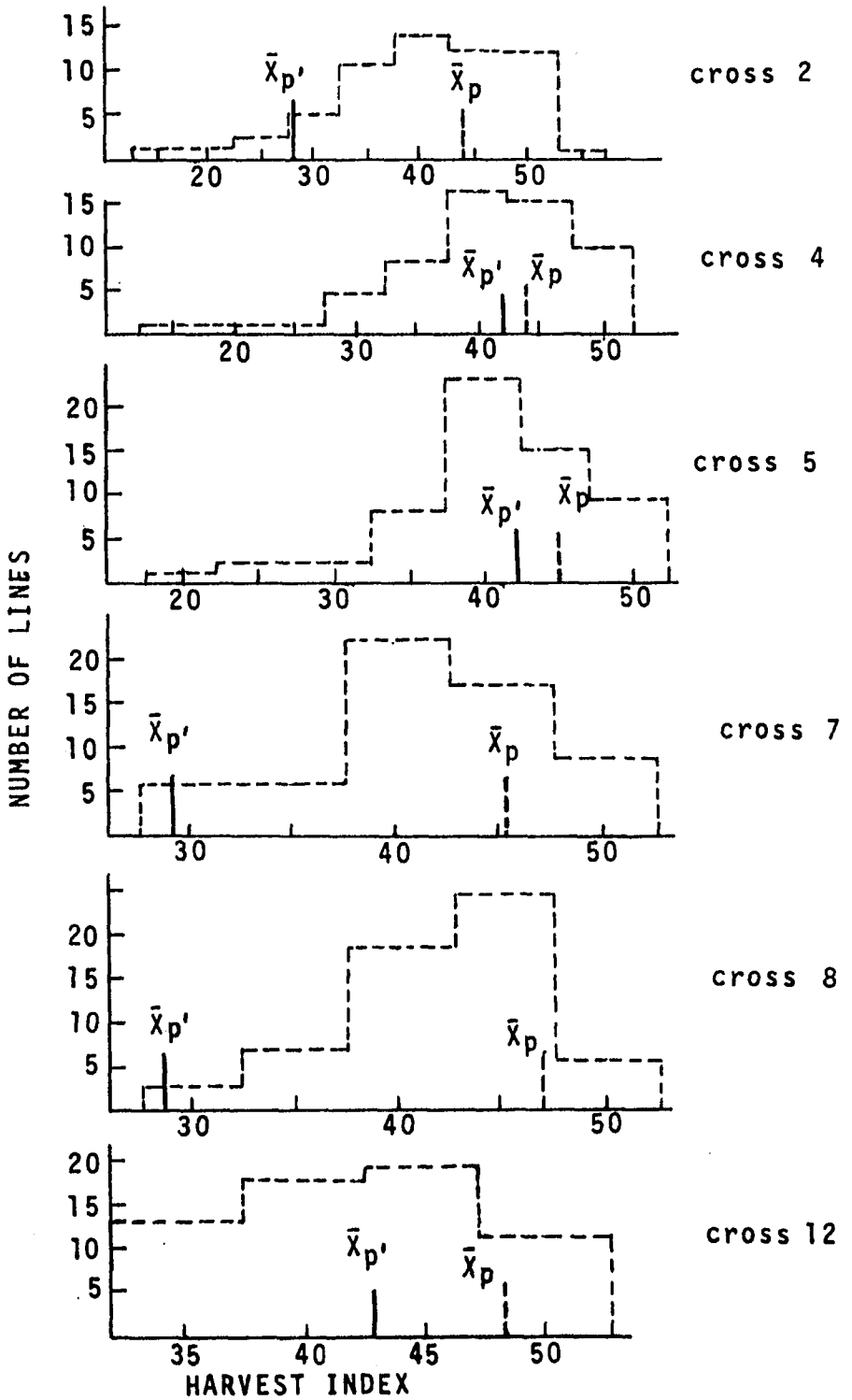

NUMBER OF LINES
BUNDLE WEIGHT
cross 2
cross 4
cross 5
cross 7
cross 8
cross 12
$\bar{X}_{p'}$
$\bar{X}_p$

Figure 5. Frequency distributions for harvest index (%) of F_2-derived lines from intra and interspecific crosses of barley evaluated in the field.


NUMBER OF LINES
HARVEST INDEX
cross 2
cross 4
cross 5
cross 7
cross 8
cross 12
$\bar{X}_{p'}$
$\bar{X}_p$

for low harvest index were from intraspecific crosses. Transgressive segregation for bundle weight was present in five of six crosses.

Most noteworthy was the transgressive segregation for high grain yield present in all crosses. Overall, 62 lines were transgressive for high yield, but only 10 for low. The highest proportion of transgressive lines for this trait occurred in interspecific cross 7.

On average, intraspecific crosses had greater proportions of transgressive segregates for heading date, bundle weight and harvest index, whereas interspecific crosses had greater proportions for plant height and grain yield.

Intraspecific cross 2 had the highest proportion of desired transgressive segregates, i.e., high yielding, early and short, and also the best transgressive segregates.

Correlation Analyses

The F_2 populations of six inter and intraspecific crosses of barley were utilized to calculate all possible phenotypic and genotypic correlations among the traits heading date, plant height, grain yield, bundle weight, and harvest index (Table 24).

The correlations between grain yield and bundle weight were the highest, whereas correlations between bundle weight

Table 24. Phenotypic and genotypic correlations among traits in each F_2 population of six interspecific and intraspecific crosses of barley; genotypic correlations are in parentheses[a]

Trait	Cross number	Heading date	Plant height	Grain yield	Bundle weight	Harvest index
Heading date	2		0.16	-0.49 **	0.19	-0.52 **
	4		0.22	-0.37 **	-0.12	-0.53 **
	5		0.06	-0.34 **	-0.28 *	-0.28 *
	7		0.66 **	0.03	0.29 *	-0.55 **
	8		0.29 *	-0.31 *	-0.09	-0.56 **
	12		-0.16	-0.33 **	-0.31 *	-0.23
Plant height	2	(0.20)		0.37 **	0.57 **	-0.18
	4	(0.28)		0.38 **	0.57 **	-0.28 *
	5	(0.03)		0.35 **	0.53 **	-0.07
	7	(0.83)		0.22	0.49 **	-0.44 **
	8	(0.38)		0.35 **	0.52 **	-0.32 *
	12	(-0.15)		0.41 **	0.68 **	-0.30 *
Grain yield	2	(-0.54)	(0.54)		0.74 **	0.54 **
	4	(-0.48)	(0.44)		0.84 **	0.49 **
	5	(-0.44)	(0.50)		0.87 **	0.56 **
	7	(-0.41)	(0.26)		0.81 **	0.20
	8	(-0.32)	(0.37)		0.90 **	0.32 *
	12	(-0.36)	(0.49)		0.87 **	0.46 **
Bundle weight	2	(-0.12)	(0.77)	(0.63)		-0.14
	4	(-0.03)	(0.71)	(0.78)		-0.00
	5	(-0.36)	(0.92)	(0.78)		0.10
	7	(0.76)	(0.63)	(0.70)		-0.34 **
	8	(0.01)	(0.60)	(0.89)		-0.03
	12	(-0.35)	(0.93)	(0.86)		0.01
Harvest index	2	(-0.61)	(-0.23)	(0.63)	(-0.18)	
	4	(-0.71)	(-0.45)	(0.50)	(-0.11)	
	5	(-0.38)	(-0.13)	(0.70)	(0.02)	
	7	(-0.65)	(-0.56)	(0.01)	(-0.67)	
	8	(-0.75)	(-0.53)	(0.31)	(-0.02)	
	12	(-0.23)	(-0.49)	(0.61)	(0.12)	

[a]Table for testing significance of genotypic correlations is not available.

* and ** denotes significance at the 5% and 1% level of probability, respectively.

and harvest index were the lowest. Genotypic correlations between grain yield and bundle weight ranged from 0.63 in cross 2 to 0.89 in cross 8, and the average genotypic correlation between these two traits was 0.77. The mean correlation between bundle weight and plant height was 0.76. In all instances the phenotypic correlation coefficients between grain yield and bundle weight, and between bundle weight and plant height were significant at the 1 percent level of probability.

In most instances, plant height, bundle weight, and harvest index were significantly and positively correlated with grain yield, whereas heading date was significantly and negatively correlated with this trait. No intraspecific cross showed significant correlation between heading date and plant height or between bundle weight and harvest index, whereas two interspecific crosses showed significant correlation between the first two traits and one showed a significant correlation between bundle weight and harvest index.

The mean phenotypic and genotypic correlations among the five traits for the intra and interspecific crosses are presented in Table 25. Except for grain yield with heading date and harvest index, and plant height with harvest index, the correlations in intra and interspecific crosses did not show contrasting difference. Grain yield was more closely associated with heading date and harvest index for intra than for interspecific crosses, whereas plant height showed greater

Table 25. Mean genotypic and phenotypic correlations among traits for intra and interspecific crosses of barley; mean genotypic correlations are in parentheses

Trait	Type of cross	Heading date	Plant height	Grain yield	Bundle weight	Harvest index
Heading date	D[a]		0.15	-0.40	-0.07	-0.44
	E[b]		0.26	-0.20	-0.04	-0.45
Plant height	D	(0.17)		0.37	0.56	-0.35
	E	(0.35)		0.33	0.56	-0.35
Grain yield	D	(-0.49)	(0.45)		0.82	0.53
	E	(-0.36)	(0.37)		0.86	0.33
Bundle weight	D	(-0.17)	(0.80)	(0.73)		-0.01
	E	(0.14)	(0.72)	(0.82)		-0.12
Harvest index	D	(-0.57)	(-0.27)	(0.61)	(-0.09)	
	E	(-0.54)	(-0.53)	(0.31)	(-0.19)	

[a]Intraspecific crosses.
[b]Interspecific crosses.

genotypic association with harvest index for interspecific crosses (Table 25).

Of greater importance for breeder is the intermediate level of genotypic correlation of grain yield with plant height and heading date.

DISCUSSION

There was a much higher frequency of significance among generation means (Tables 5 and 6) in the field experiments than in the controlled-environment experiment, even though the same crosses of barley were involved in both conditions of testing. Probably these differential results were due to the differing degrees of precision obtained for the two conditions of experimentation. The coefficients of variation (CV) (Tables 26 and 27) showed that the field experiments were much more precise than was the one grown in the controlled-environment chamber. For example, the mean CV's for heading date were 2.8 and 6.7 percent for the field and controlled-environment experiments, respectively; for plant height, they were 4.6 and 7.4 percent, respectively; for grain yield, they were 25.7 and 33.6 percent, respectively; and for harvest index, they were 13.0 and 23.9 percent, respectively. Thus, for all cases where a trait was measured in both experiments, the mean CV was much lower in the field experiment. The greater precision for the field experiments likely was attributable to the greater sample size used, that is, a plot in the controlled-environment experiment was a single plant, whereas a plot in the field experiments contained 15 plants.

For the generation-mean analyses I used the data as collected on the arithmetic scale. The original data from the

Table 26. Coefficients of variation for six traits measured in twelve crosses of barley in the controlled-environment chamber experiment

Cross number	Trait					
	Heading date	Plant height	Grain yield	Straw yield	Harvest index	Panicles per plant
1	4.7	6.4	25.1	20.2	25.4	32.8
2	5.6	7.7	39.0	13.8	31.8	19.8
3	5.7	6.2	37.8	27.2	32.4	28.8
4	5.1	7.7	25.5	21.3	7.4	32.9
5	6.3	8.6	39.2	24.1	18.7	33.6
6	5.0	8.5	38.9	27.2	27.9	37.9
7	8.5	6.9	34.1	28.0	34.3	18.7
8	7.3	5.8	36.4	21.1	30.2	17.8
9	8.5	7.5	32.9	26.8	33.5	26.1
10	10.7	5.3	31.4	21.2	19.6	21.6
11	5.4	10.6	32.8	19.0	26.5	34.5
12	7.8	7.3	30.1	19.8	18.9	18.5
Mean	6.7	7.4	33.6	22.5	23.9	26.9

Table 27. Coefficients of variation for six traits measured in twelve crosses of barley in the field experiment

Cross number	Trait					
	Heading date	Plant height	Grain yield	Bundle weight	Harvest index	300-seed weight
1	2.8	3.6	19.5	17.1	10.4	7.2
2	2.5	4.0	30.2	30.9	16.4	8.7
3	1.9	3.3	23.0	20.1	9.6	7.0
4	2.5	5.5	25.5	15.3	17.4	5.2
5	3.0	3.6	28.9	24.9	10.5	6.5
6	1.5	3.8	23.1	23.0	15.1	5.6
7	4.0	5.0	20.6	21.2	12.5	7.5
8	4.2	7.3	29.6	23.8	14.9	9.3
9	2.5	3.9	28.8	23.8	12.3	10.2
10	3.4	4.8	27.4	25.8	9.6	8.1
11	4.0	7.0	26.6	27.5	17.5	9.2
12	1.7	3.6	25.4	22.2	10.3	6.4
Mean	2.8	4.6	25.7	23.0	13.0	7.6

various generations were normally distributed so there was no reason to transform them to another scale. Further, Mather and Jinks (1971) have said that the scale to be used for this type of analysis is really a matter of expediency because the theoretical considerations of the scale to use have not been worked out. Lawrence (1974) also pointed out that the scale employed in measuring a plant trait usually was the one found to be most convenient, and that really it must be chosen empirically.

The several genetic assumptions that underlie the model for the Hayman method of generation-mean analysis were outlined in the Materials and Methods section. The first assumption, of course, was fulfilled because both H. vulgare and H. spontaneum have the diploid number of chromosomes (i.e., $2n = 14$). The second assumption for the generation means analysis was that the most positive alleles for a trait occurred in one parent and most negative ones in the other. Of course, this assumption was not satisfied because for each trait I found that one to several plus factors were contributed to F_2 segregates by both parents in all crosses (Table 21). Therefore, the additive genetic effect (i.e., [a]) probably was underestimated. The third underlying assumption of generation means analysis was that linkage among contributing genes was negligible. Linkage, if present, could bias the parameters estimated by this model. My study did not in-

clude the four double backcrosses required to test for the presence of linkage. Because the number of effective factor pairs estimated for the various traits in my barley crosses was almost always less than the diploid number of chromosomes for the species I used, it is unlikely that linkage, especially, the repulsion phase, existed between plus and minus factors for a trait. Thus, linkage probably was not a serious factor contributing to bias from the generation-means analysis.

The generation-means analysis was applied only to those parental combinations that showed significant variation among the mean values for the various generations tested. Generally, the digenic model, which included estimates of the effects of additivity, dominance, and three types of epistasis, did not provide a consistent picture of the predominant type of gene action that operated for any one trait, or differential gene effects for intra versus interspecific crosses. Even though only one cross-trait combination of the many I analyzed showed a significant Chi-square for goodness-of-fit to the digenic model, few significant estimates for the genetic parameters were detected. A contributing factor to my inability to find significant estimates for genetic parameters may have been the failure of segregating factors to be isodirectionally distributed between the parents in a cross. The Chi-square to measure goodness-of-fit for plant

height in cross 11 to the digenic model was significant. This could have been attributable to the presence of higher order epistasis or to linkage or both.

There were two instances where a general trend for type of gene action was apparent over most or all crosses. In the first case, additive genetic effects were more prevalent and important than were nonadditive ones for heading date. It is noteworthy that these results are consistent with those reported by Riggs and Hayter (1975) who found that heading date in spring barley showed large additive effects. Secondly, epistatic genetic effects tended to be of more importance than the nonepistatic ones for 300-seed weight.

It is worthy to note that in the generation-means analysis, significance for the genetic effects of additivity and (or) dominance is most meaningful when epistatic effects are absent. It follows that when significant additive and dominance effects are accompanied by significant epistatic effects, the estimates for the first two types of gene action are apt to be biased due to the confounding effects of epistasis.

Of greatest importance to my study was the fact that intra and interspecific crosses of barley showed no differences in types of gene action responsible for the inheritance of several traits.

Little research has been reported to relate heterosis of

agronomic traits to specific genetic effects in barley. But knowledge of the relative importance of the several types of gene action is very important if a breeder is to make sound decisions in planning his breeding program. Several studies have reported evidence of heterosis for many agronomic traits, but none has estimated components of heterosis (Immer, 1942; Suneson and Riddle, 1944; Upadhyaya and Rasmusson, 1967; and Stolen, 1974).

Generally, for barley breeding, heterosis would be considered desirable for all traits that I measured, except for plant height. There was significant heterosis for grain yield in five of six interspecific crosses when tested in the field experiment, whereas no intraspecific cross showed significant heterosis in either environment. Also, the mean heterosis was 84 percent for interspecific crosses versus 57 percent for intraspecific ones. And, interspecific crosses exhibited a wider range of heterosis than did intraspecific crosses for this trait. The amount of heterosis exhibited for grain yield was not as high as that reported by Stolen (1974) but greater than those reported by other authors (Englewown and Pal, 1934; Immer, 1941; Suneson and Riddle, 1944; Hagberg, 1953; Aastveit, 1961; and Suneson, 1962).

Heterosis for earliness in heading date was shown in all crosses in both types of experiments. The average and range of heterosis for this trait are about the same in the field and

controlled-environment experiments for both intra and interspecific crosses. Also, there was no difference between field and controlled-environment experiments in the average and range of heterosis for plant height and harvest index in inter and intraspecific crosses, respectively. There was a slight difference between intra and interspecific crosses in the average heterosis for bundle weight. For number of panicles, even though the percentage of significant cases of heterosis was greater in inter than intraspecific crosses, the average and range for heterosis was similar in both types. The average heterosis for 300-seed weight was slightly greater in interspecific crosses. However, the ranges and the percents of significant cases of heterosis for this trait were similar.

The genetic causes for heterosis or heterobeltiosis in a particular trait-cross in some cases could be explained by the presence of significant dominance and (or) digenic epistatic effects. For example, in crosses 7 and 8, significant dominance effects determined heterosis for grain yield and heading date, respectively. Also, in cross 7, significant dominance effects determined heterosis in bundle weight. Heterobeltiosis for number of panicles in cross 8 corresponded with a highly significant positive dominance effect. Heterobeltiosis, expressed for heading date in cross 12, was associated with significant and negative dominance effect. The

amount of heterosis exhibited for heading date in cross 6, for plant height in cross 4, and for straw yield in cross 2, could be explained by the genetic effects estimated from digenic models.

Clearly, there were several ways in which heterosis could arise. If a digenic epistatic model was considered, positive heterosis could occur when [d] + [dd] was positive and greater in magnitude than [a] + [aa], whereas negative heterosis could occur when [d] - [dd] was negative and greater than (-[a] + [aa]) according to Mather and Jinks (1971). In my study, however, heterosis could not be assigned uniquely as being due to additive, dominance, and epistatic components. Heterosis is a complex genetical phenomenon which depends on the balance of different combinations of gene effects as well as on the distribution of plus and minus alleles in the parents of a cross. The frequency distributions of grain yield, bundle weight, and harvest index (Figures 3 to 5) for the six F_2 populations showed unimodality and continuity, which suggest polygenic inheritance.

The estimated number of effective factor pairs that controlled heading date and plant height in my crosses, i.e., about 3.0, was in agreement with results reported by previous investigators (Neatby, 1929; Hehn, 1948; and Ubisch, 1919). The number of effective factor pairs estimated by the Castle-Wright formula for heading date in crosses 2 and 7 and plant

height in crosses 4, 5, 7, and 12 was verified by factorial genetic analysis. That is to say, when the minimum numbers of effective factor pairs estimated by the Castle-Wright formula were used in factorial genetic analyses for these cases, non-significant Chi-squares were obtained for goodness-of-fit. However, when the number of factor pairs for heading date in cross 8 and harvest index in cross 12 were checked by factorial genetic analysis, the Chi-square values were significant, and thus, the results obtained by Castle-Wright formula were not verified. A possible cause for such contradictions could be that the genetic components of variance were overestimated. An effective factor pair detected by the Castle-Wright formula may have represented a single locus, a cluster of linked loci or even a whole chromosome. Both bundle weight and grain yield were more complexly inherited, with the average number of segregating loci for these two traits being 5.5 and 6.0, respectively. For each trait-cross case, the number of pairs of effective segregating genes in the F_2 populations, probably was underestimated because one or more assumptions underlying the Castle-Wright formula were not satisfied. Therefore, it would not be unusual for the estimated number of effective factor pairs from the Castle-Wright formula to be either less than or equal to the haploid number of chromosomes of the species under study.

Obtaining unbiased estimates of the minimum number of ef-

fective factor pairs that condition a trait via the Castle-Wright formula is based on several assumptions. The first assumption of equal contributions from all segregating loci was unsatisfied in some trait-cross cases as evidenced in cross 2 for heading date, and for plant height in crosses 4, 5, and 7. When this assumption is not satisfied, the formula gives values that are smaller than the actual number of segregating factors. The second underlying assumption of the Castle-Wright formula, i.e., no linkage among contributing genes, has been considered previously in generation-mean analysis. The assumption that all plus and minus alleles are distributed isodirectionally between the parents was not satisfied in my material. Therefore, the numbers of segregating loci probably were underestimated. The assumptions of no epistasis and that either no dominance occurs or the degree and directions of dominance of plus factors was similar for all loci probably were not satisfied as evidenced in Tables 7-8, and Tables 19-20, respectively. Presence of dominance or epistasis inflates the genetic variance in the F_2 and leads to an underestimation of the number of segregating loci. However, even though these assumptions may not be satisfied, the information provided by the Castle-Wright formula can be of value to the plant breeders who are aware of the formula's limitations. According to Mather (1949), the number of genes involved in the inheritance of a complex charac-

ter is of great importance in predicting the "minimal limits" and "rates of advance" under selection.

It is noteworthy that the H. spontaneum parents contributed plus factors to F_2 segregates for all traits I studied. Thus, for all traits H. spontaneum contributed some genes that could be used to improve cultivated barley. In some instances, e.g., harvest index, the H. spontaneum parent seems to contribute more plus factors than did the H. vulgare parent, and in most instances it contributed at least one plus factor.

I used the populations of F_2-derived lines from the six barley crosses in a simulation exercise to obtain the probability of the occurrence of superior agronomic lines. Basically, the methodology used was one of selection by independent culling level. A superior F_2-derived line from an interspecific cross would be one with yield 30 percent above the best parent and equal to the H. vulgare parent in harvest index, plant height, and heading date. In all interspecific crosses the best yielding parent was the H. vulgare line, and improving upon it by 30 percent required the addition of from one to three plus factors from H. spontaneum. The same culling levels were used for the populations of F_2-derived lines from intraspecific crosses, but because both parents in these crosses were agronomically sound, I used culling levels of 30 percent above the better parents for yield and the means of

the lower, higher, and lower parent as the culling levels for heading date, harvest index, and plant height, respectively. The results of this exercise are presented in Table 28. Superior F_2-derived lines in the intraspecific crosses occurred with proportions between zero and 1.7 percent, whereas for interspecific crosses, 36.7, 20.0 and zero percent of the lines were superior. The high proportion of F_2-derived lines selected as superior by the independent culling level method in some crosses was associated with high frequencies of transgressive segregates for high grain yield, earliness, and shortness.

Next, culling levels were converted to number of plus factors required in the superior lines. Then I assumed equal gene frequency for both plus and minus alleles and independent segregation of genetic factors and calculated the theoretical probabilities of obtaining superior F_2-derived lines in Bc_0, Bc_1, and Bc_2 generations. To do this, the formulas presented by Jennings (1916) and Anderson (1949) were extended to the situation of several loci dispersed in both parents. Heading date was not used as a selection criterion for these calculations because selection for high grain yield and high harvest index selected indirectly for this trait. The theoretical probabilities for superior lines in the six barley crosses are presented in Table 28. The probability of the occurrence of superior lines was lower for Bc_0 than for Bc_1 in

Table 28. Percentages of superior F_2-derived lines in the Bc_0 generation, numbers of factor pairs required in superior F_2-derived lines, and theoretical probabilities of the occurrence of superior F_2-derived lines in Bc_0, Bc_1 and Bc_2 generations

Cross number	Percentage of F_2 lines selected	Number of plus factor pairs in superior lines for:			Theoretical probability of selecting superior lines in generations:		
		Grain yield	Harvest index	Plant height	Bc_0	Bc_1	Bc_2
2	1.7	4[a]	5[a]	9[b]	5×10^{-6}	2×10^{-5}	2×10^{-7}
4	0.0	7	5	6	1×10^{-7}	2×10^{-5}	7×10^{-6}
5	1.7	7	4	8	2×10^{-7}	2×10^{-6}	9×10^{-7}
7	36.7	8	4	8	2×10^{-5}	4×10^{-6}	4×10^{-6}
8	20.0	5	5	8	2×10^{-6}	5×10^{-6}	5×10^{-7}
12	0.0	5	3	9	2×10^{-5}	4×10^{-5}	6×10^{-6}

[a]Minimum plus factor.
[b]Maximum plus factor.

all three intraspecific crosses, whereas the probabilities for the interspecific crosses were similar for the two generations. The theoretical probabilities for Bc_2 were lower than those for Bc_1 in all crosses except cross 7. The theoretical probabilities of obtaining superior lines indicated that Bc_1 was the best generation for selection in all crosses except cross 7 in which case the Bc_0 was best.

The significant kurtosis value indicated that all F_2-derived line distributions had deficiencies of lines in the flanks and excesses of lines in the tails of the distribution: Thus, there would be an excess of lines that likely would be transgressive segregates. And, in all instances except plant height in cross 4, bundle weight in cross 8, and harvest index in crosses 7 and 8, transgressive segregates were evident (Figs. 1 to 5 and Tables 22 and 23). Transgressive segregation for heading date was consistent and more frequent for earliness than for lateness. From theoretical considerations, it would be expected that the number of transgressive lines would increase as the genes of plus effect are more equally dispersed between the parents. That is, the maximum frequency of transgressive lines should be obtained when plus factors are equally shared between the parents of a cross or when both parents had similar mean values.

Transgressive segregation for grain yield occurred in all crosses and much more frequently for high yield than for

low yield. The highest yielding segregates occurred in intraspecific cross 2, and these would be very useful in short term barley breeding programs. However, the greatest frequency of transgressive lines occurred in the interspecific cross 7. To grasp the significance of contrasting the best yielding segregates versus the highest frequency of transgressive segregates, refer to Table 23. The highest yielding segregate was 51 g per plot, and this occurred in the intraspecific cross 4, whereas the highest proportion of transgressive segregates for high yield occurred in the interspecific cross 7. Yet the highest yielding segregate in cross 7 produced only 47.7 g per plot.

Genotypic correlations indicated either pleiotropism or close linkage between loci that condition two traits. Grain yield was positively and significantly correlated with plant height, bundle weight, and harvest index and negatively and significantly correlated with heading date. These correlations are in agreement with those reported by previous researchers (Grafius, 1938; Kohl, 1930; and Robertson and Koonce, 1936). Correlations between heading date and plant height reported in my study, however, disagree with those presented by David (1931). I would expect to improve grain yield in barley by selecting for early heading date because of the negative correlation between these two traits. Short barley plants are usually desired to give lodging resistance, however,

its positive genotypic correlation (0.41) with grain yield indicates that it might be difficult to produce a short barley variety with high grain yield. The high genotypic correlation between grain yield and bundle weight (0.84) and the intermediate correlation between grain yield and harvest index (0.43) suggest the use of these traits as additional criteria for selecting for yield.

My study indicated that H. spontaneum posseses potentially useful genes which could be incorporated into the barley varieties. Actually, H. spontaneum has been used in barley breeding programs. Currently, resistance to powdery mildew from this source is proving of value. However my results suggest H. spontaneum could be used as a source of genes for improving productivity also.

The interspecific crosses indicated that all three H. spontaneum strains I used contributed useful genes, even though there was no indication of the presence of such genes from direct observation of the lines themselves. Because these H. spontaneum parents proved to be useful sources for grain yield genes, it would seem worthwhile to investigate the genetic potential of additional H. spontaneum genotypes. Of course, the use of H. spontaneum as a source of germplasm in barley breeding would bring two objectionable traits, i.e., shattering seed and two-rowed spikes. However, these traits could be eliminated easily because both are simply inherited.

The suggested approach for using H. spontaneum genes for productivity in short and long term breeding programs would be:

(a) for a short term program, a large number of Bc_0F_2 or Bc_1F_2-derived lines from H. vulgare x H. spontaneum crosses would be tested, and then the selected lines would be used for further crossing with other varieties and subsequent selection. Or, H. spontaneum could be used as donor parents with extensive backcrossing to the H. vulgare genotypes,

(b) For the long term barley breeding program, several H. vulgare and H. spontaneum genotypes should be crossed and backcrossed to the H. vulgare parent. To permit genetic recombination to occur from several sources of H. vulgare and H. spontaneum the backcross F_1's could be combined by successive cycles of crossing into composite crosses. The segregates from the composite crosses could be used as the materials for initiating population improvement.

SUMMARY

Six generations in each of six inter and six intraspecific crosses of barley were grown in controlled-environment chamber and field experiments to estimate the types and magnitudes of genetic effects that were involved in the inheritance of heading date, plant height, straw yield, grain yield, harvest index, number of panicles, and 300-seed weight via generation-means analyses (Hayman, 1955). Also, six F_2-derived line populations and their parents were tested in an adjacent field experiment. From this experiment, estimates were made of the minimum number of effective factor pairs determining each trait, phenotypic and genotypic associations between pairs of traits were computed, and frequencies and magnitudes of transgressive segregates were determined for heading date, plant height, grain yield, bundle weight and harvest index.

Heading date was controlled by a few gene pairs (probably about 3.0) that exhibited primarily additive gene action. Some nonadditive gene action was detected for this trait, however, H. vulgare and H. spontaneum parents both possessed alleles for early heading. Plant height was controlled by three to four genes that exhibited both additive and nonadditive gene action, and both H. vulgare and H. spontaneum parents contributed alleles for short height. Grain yield and bundle

weight were controlled by five or more factor pairs each. For these traits, neither additive, dominance or digenic epistatic effects were significant very often which suggests that the genes determining them had a higher order epistasis or linkage or both. Harvest index was controlled by about four genes that had predominantly additive gene action. The importance of epistasis varied among traits, being more important for 300-seed weight and heading date, and least important for harvest index, grain yield, and plant height.

Heterosis for grain yield and heading date was of greater mean magnitude in inter than in intraspecific crosses in the field experiment. In some trait-cross cases, dominance, digenic epistatic and higher order epistatic effects may have been the possible genetic causes of observed heterosis or heterobeltiosis. The high heterosis reported in my study emphasizes the potential value for utilizing hybrid vigor in barley.

Transgressive segregates were obtained for all traits in both intra and interspecific crosses and those involving grain yield may provide the basic materials for improving the productivity of barley varieties.

All three H. spontaneum strains used in my study contributed one or more useful genes for grain yield, heading date, plant height, bundle weight, and harvest index. Therefore, it seems that H. spontaneum can be a useful source of favorable

genes for quantitative traits, especially for grain yield, which can readily be incorporated into barley varieties by backcrossing.

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